INFORMATION TRANSFER BETWEEN FORAGING ANIMALS: THE CONSEQUENCES OF ATTENTIONAL LIMITATIONS

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September 2005

ACKNOWLEDGEMENTS

Firstly, I would like to give my sincerest thanks to Graeme Ruxton and Mark Broom, who supervised this PhD project. Thank you so much for offering this project to me, and for supporting, encouraging and guiding me through it. Neither mathematics nor computer modelling was, is, or ever will be my forte, so it was an incredibly brave move. We've had some interesting and extremely trying moments, and there are several times when you must surely have tempted to just throttle me – but you've been patient and somehow we managed to get through it. I've come a long way in the last three years (well presumably, anyway) and I owe you both a lot. Thank you!!! I could not have done it without either of you and I am immensely grateful.

I would similarly like to thank both the University of Glasgow and the University of Sussex for looking after me and making me welcome throughout my stay at both. Studying and travelling between two universities that are effectively at opposite ends of the country has not made things easy, but the process was surprisingly painless most of the time. I must also thank the Natural Environmental Research Council for generously funding this project and providing me with the resources to do some foraging of my own.

There are many people who have made their contribution in some way or other over the last three years, and I will try to remember them all here:

Andrew Jackson – I thank you eternally for being the nerd that you are. Your technical advice (and our 'secret' outings) have been truly invaluable to me, and I appreciate it more than I can say. I owe you a pie or two. Jan Lindstrom, thank you for the many evenings we spent in my first year discussing countless topics of varying scientific content and quality, for giving me ideas, advice, encouragement and for generally being enjoyable and stimulating company (mentally and hepatically).

Jo, Andrew, Richard, Tom, Lesley, Sarah, Colin, Nick, Fiona, Martin, and all the various other people who I've had the pleasure of sharing my lab with at some point over the last three years - thank you for all your help and advice, and for making

Glasgow an enjoyable and friendly place to work. Thank you also for not moaning too much about my drumming on the desk.

Chris Pendlebury and Helen Gorman, Claire Inness, Craig Walling and Clare Stamper, Mike Fisher, Chris Foote, Dan Haydon, Kate Arnold, Stuart Humphries, Jon Crane, Lucy Webster and Dr Dave, Tom Ford, Gill Taylor, David Alvarez, and the many others within or loosely associated with the department, who have made for entertaining and pleasurable nights out. Thank you to all the people who took the time to proof-read various parts of this work, and for pointing out potentially embarrassing spelling mistakes involving the term "public information".

My parents and family, who have supported me and shown belief throughout, and at least *pretended* to understand what I was talking about. Jo Mould and Diane Baum, for being kind, friendly, tolerant, at times formidable, but at the very least understanding flat-mates. Berkeley2 practice studio, and also Tim, Scott and Craig of the yet-to-be-famous 'This Pig Flies', who have given me a vent for my frustration and creative (tortured-artist) complex. It's quite possible I would have imploded long before reaching this point had it not been for you guys. Cheers!

Monica, for your fantastic cooking and generous helpings. Wendy, Ryan, Heather, Martin, and all my other random gigging-partners. And everyone else I've met along the way - real, virtual or imaginary – who, for better or worse, have made things that little bit more interesting.

Lastly and perhaps most of all I'd like to say thank you to two very special: Carina Mansey, thank you for being the truest of friends; you were there when I needed one and didn't have much else. I am forever grateful to you. And finally Katie Grape, thank you for being amazing and wonderful in every way imaginable. This last year has been the best in memory. Thank you for everything. Thank you for being alive. This thesis is dedicated to you.

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SUMMARY

Since its inception during the 1960's, optimal foraging theory has become a popular and well-studied field in behavioural ecology. A vast expanse of empirical work has been carried out to investigate whether animals forage optimally, and how they achieve this. Researchers have also used a range of theoretical techniques to predict the behaviour of animals foraging under various ecological conditions. Particular attention has been paid to animals feeding in isolated and depleting food patches, and the length of time they should be willing to spend feeding in such patches before quitting to move to the next (patch residence time, or PRT) in order to maximise long-term prey capture rates. The modelling work presented in this thesis examines further, various aspects of optimal foraging theory, investigating PRT and the long-term foraging success of group foragers.

A contentious theory attracting much research, is that individuals foraging in groups which share information regarding the successful capture of food resources may be better off than when not sharing such information, or when foraging alone. This use of public information (PI) allows them to acquire information relating to the quality of a food patch more quickly. At any one time they will have better knowledge of the decreasing patch quality, and be able to make a more accurate estimate of when to quit and move to another patch. I demonstrate that animals sharing such information do indeed experience benefits over groups that do not share public information, but *not* over lone foragers. This suggests that although PI itself is not likely to promote the formation of animal groups, in an environment where animals have already formed cohesive groups (for example where predation risk is high) sharing PI offers a further advantage to them.

This model, and others before it are based upon a formula which calculates an estimate of the number of prey remaining in a food patch, depending upon the distribution of prey resources throughout the environment, the length of time spent by

foragers in a food patch, and the number of prey discovered there. When foraging in groups, this model assumes that each forager keeps a track of the total number of prey caught in a patch by inferring its own foraging success on to each other forager in the group. As group size increases this is likely to be more and more unrealistic, because although prey is likely to be discovered more quickly, each forager faces a lower chance of finding any. I present an alternative model that removes this bias in large groups. I demonstrate that using this new estimator, foragers are generally better able to estimate patch quality when in large groups, but their ability to do so is more variable from patch to patch.

I further modify the basic public information models developed early in the thesis, to consider the constraints imposed upon animals by their limited cognitive and sensory resources. Animals do not have the powers to perceive and process information from all sources at once – this is restricted by the relative size of their brain, their sensory fields, and various external factors such as interference in the environment. The information an animal receives is in many cases therefore unlikely to be perfect, or cost free. I develop two models to investigate this. Firstly, I examine the extent to which public information remains beneficial when animals must pay a cost for its acquisition, in terms of divided attention. It has been shown that animals dividing their attention between a number of tasks suffer a reduced performance at each one (Vreven and Blough, 1998; Dukas and Kamil, 2000). My model examines foragers dividing their attention between personal foraging, and scouting for public information signals. The cost to public information use is incurred as a reduced personal foraging success. I show that as public information becomes more costly, the success of foragers decrease; but not in the way predicted by common sense. There remains a point at which information is acquired by foragers, where they do not pay for it. This is an artefact of time spent travelling between patches – costs are only encountered while foragers are in a patch, whereas reduced personal foraging efficiency affects the *total* time spent foraging. The two increase disproportionately to one another, and leads to cost-free public information above a certain point.

The second model examines the effect of public information that may be inaccurate or incomplete. A consequence of limited attention is that an animal is likely to make mistakes concerning the acquisition of information. Movements or sounds partially

or totally unrelated to foraging may be interpreted as information signals, whilst true signals may be lost altogether – particularly in large groups. This model investigates how both these types of error may affect the long-term foraging success of animals in sharing public information. My findings reveal that although errors of both types are detrimental to foraging efficiency, the relative effect of creating false signals is considerably greater than that of missing true signals. In an environment where the food supply is unpredictable, it is easy to over-estimate the quality of a food patch, and waste valuable foraging time in unprofitable patches. On the other hand, under-estimating a food patch will not be too harmful most of the time because in rich patches more food will be discovered relatively quickly, and in poor patches this will simply aid patch departure.

Non-spatial models of foraging behaviour have in the past neglected some serious considerations of animal movements in the environment. It has often been assumed that animals discover food patches at a rate that is proportional to their group size. This is often a useful simplification to make for practical purposes, but is unlikely to be true in most natural circumstances. Their true rate of patch discovery will depend on their dispersal from one patch, into the environment. As foragers become scattered, each will subsequently have to travel further to a newly discovered patch. The further a forager has to travel, the less food it will receive once it gets there, since the patch will already be partially depleted. Once a forager is beyond a certain distance, it will no longer be beneficial for that forager to join the patch, and it should continue searching for its own. I examine how various factors of the group and the environment affect this critical joining distance. I show that although overall prey abundance in the environment affects the foraging success of each individual, it does not have any effect on the critical joining distance. I also show that a forager will find patches less attractive as forager density increases, and with higher searching rate within patches. But they should find patches more attractive if they are able to travel more quickly to patches once they have been discovered.

The work in this thesis offers insights into several aspects of social foraging theory, with particular emphasis on public information sharing. With the models presented here, I make predictions that can be tested empirically to give us a deeper understanding into why animals share public information, the benefits and obstacles

they face by doing so, and the obstacles they must overcome when feeding in groups. These models provide a framework that can in the future be adapted to make predictions for specific ecological systems, but can also be combined or modified further for a more complete investigation into the behavioural ecology of social foraging under cognitive constraints.

CHAPTER 1

GENERAL INTRODUCTION

Animals require food to survive. In the natural world food resources are rarely dispersed homogenously throughout the environment, but are more commonly found in clumps, or patches. Being mobile suits many animal species because it enables them to move around and search for these food patches. However, animals are constrained in the time they have available for feeding because they must also perform a host of other behaviours crucial to survival and reproduction. It is therefore important that animals maximise the amount of food they can obtain, in the shortest time possible. This is the essence of optimal foraging theory.

The work presented in this thesis is an important contribution to the field of behavioural ecology, for several reasons. Optimal foraging theory is one of the principal progenitors of behavioural ecology, and perhaps because feeding behaviour is of such undeniable importance for the survival of just about every species mentionable it is often entwined with many other aspects of behaviour. Foraging has implications for not only personal survival, but also for reproduction, courtship and mate selection, population growth, and territoriality along with countless other behaviours - including, as I describe here, information sharing and flocking. This thesis evaluates some of the underlying assumptions made by previously accepted optimal foraging models, and also examines these last two behaviours in this list, their mutual relationship with each other and the ultimate consequences they may have on each other and on foraging behaviour. I note that some assumptions made by previous models are not necessarily ecologically realistic and I discuss the likely significance of this for animals foraging within groups, and for animals attempting to utilise the resources in their environment to the fullest. I present models that provide further evidence in an attempt to explain currently observed animal behaviour, and which can be easily adapted to predict and test behaviour in future empirical studies.

In 1976, Eric Charnov published a theoretical model that predicted how much time an animal should spend feeding in a food patch, before quitting and moving onto the next. He noted that an animal should only remain feeding in a food patch until its feeding rate fell to the average rate it would expect to experience in the environment as a whole. If the forager remained in a patch longer than this, it could be doing better by moving elsewhere, and if it quit the patch before this it would be wasting a profitable opportunity. This is called the marginal value theorem (Charnov, 1976) –

the marginal value is the average rate of gain for the environment, and therefore also the level of prey at which patches should be quit.

As an animal feeds it depletes the available resources in the patch, making them harder to come by, until at some point it is more costly for a forager to remain searching where it is, than to move elsewhere. The point at which a forager quits a patch is dependent upon two things:

1) The average quality of each patch (how much food is present there).

2) The average time spent travelling between patches (called travel time).

The average patch quality determines the richness of the environment. As average patch quality increases, the average rate of gain also increases. If the marginal value is higher, the patch quitting value increases as a result. Travel time has the reverse effect. Increasing the average travel time between patches lowers the average rate of gain of the environment because a longer time is spent without obtaining food. The marginal value decreases, and so the patch quitting value decreases also. Krebs et al (1974) and Cowie (1977) provided the first experimental evidence that this is what occurs in nature, using captive-bred black-backed chickadees (*Parus atricapillus*) and wild-caught great tits (*Parus major*), respectively. There is a further wealth of empirical evidence to show that animals do indeed tend to forage optimally (e.g. Pulliam, 1980; Lima, 1985; Alonso et al, 1995; Tenhumberg et al, 2001; Enderlein et al, 2003; Wimmer and Whitehead, 2004; White et al, 2005).

It is well known that many animals live and feed in groups (Krause and Ruxton, 2002). One of the myriad theories proposed to explain the aggregation of animals is that of information sharing. By sharing information about the availability of resources, each individual should be able to make an up-to-date estimate of the state of the environment it resides in, more quickly than if it were on its own (Clark and Mangel, 1984, 1986; Valone and Templeton, 2002). Using social information for the estimation of environmental quality in this way is termed public information use, or PIU (Valone, 1989). In terms of foraging, animals sharing information about the availability of food resources in patches that are outwardly similar, should have a better appreciation of the state of prey depletion within each patch it visits (Valone, 1989). When feeding, foragers may not necessarily know the quality of a food patch. Often the prey may be hidden or cryptic. The only way foragers can estimate the

quality of a patch in such a situation is by sampling, i.e. as they search for food. They may have an expectation of average patch quality that they have gained through previous experience, and they update this estimate continuously when feeding. However, if foragers take note of the success of other foragers close to them and combine this public information with their own sampling information, they have at hand a vast pool of up-to-date information relating to patch quality. With this information they should be able to estimate the patch quality much more quickly, than if they were relying purely on personal sampling.

Bayes' theorem has been used frequently as a tool for optimal foraging models. Bayesian models such as Iwasa et al's (1981) estimator, baesd upon Charnov's (1976) marginal value theorem, have proved very useful in studying and predicting the behaviour of foraging animals. Indeed, Bayesian decision theory is well suited to foraging theory. It assumes that an individual has a 'prior' knowledge or expectation of the state of the environment. In this case, for example, it will be the average value of food patches. It then assumes that the individual uses sampling information to update this prior, into a 'posterior' expectation of the current situation – i.e. the quality of the food patch a forager is feeding in at this particular moment in time. As a forager searches for food it is constantly updating its posterior, which becomes the new prior, and so on. Public information models simply assume that an animal is able to update this information more quickly than individual foragers, because it is acquiring sampling information from several sources at once.

After the early-1980's, perhaps as a result of the the agreement of so many experimental studies with Charnov's (1976) marginal value theorem, the study of optimal foraging theory suffered a decline. Many researchers seemed to lose interest now that optimal foraging had been 'solved'. Thanks chiefly to Valone and a handful of others, it was realised by the mid-1990's that foraging behaviour had not expired afterall and that foraging behaviour was more prevasive than previously thought. Many doors remained unopened. It was recognised that animals were not omniscient and did not exclusively feed alone. Nor did they have an unlimited time to perform their feeding behaviour, because there were a whole series of other behaviours which also contributed to their survival. This resurgence continues to this day, and it is a more exciting time than ever to be involved with foraging theory. The fields of

psychology, ecology, ethology and mathematics are communicating and cooperating like never before, allowing many new opportunities for study to arise. This is particularly important for the theoretician, as it helps to ensure the development of models that do not drift too far from reality in attempt to retain simplicity and tractability.

Using a simple Bayesian model, Valone (1993) examined the benefits of public information use within foraging groups. He imagines an environment in which tightly cohesive groups of foragers travel between a series of isolated food patches, each containing an unknown number of prey items. Upon feeding, these prey items diminish and the patch becomes depleted over time. Using a modified version of a model developed by Iwasa et al (1981) to estimate the decreasing quality of food patches; Valone simulates foraging activity by groups sharing public information, their consequent ability to quit patches at the marginal value, and their resulting long-term foraging success. In this thesis I pick up this work and develop it further, exploring the limitations of public information use between animals (Chapters 5 and 6), and limitations of the model itself (Chapters 3 and 4).

In Chapter 3, I re-evaluate the assumptions made by Valone (1993). Although based heavily upon the predictor developed by Iwasa et al (1981), Valone inadvertently makes a number of assumptions that depart from this model, thus creating internal inconsistencies between the two. I attempt to rectify this with a mathematical model once again based upon Iwasa et al's (1981) predictor, but removing the inconsistencies introduced by Valone. I re-examine the predictions made by Valone's model, where foragers share information of all successful prey capture events. I consider the benefits to long-term foraging success for groups sharing public information, and the implications of not sharing public information - in particular I examine the importance of patch departure decisions, and consequences of conflict over patch quitting in groups of individuals which do not share the same patch estimate but must remain within the foraging group.

Some animals may form very large groups. Some bird flocks, for example, can easily contain dozens of individuals (Poulsen, 1996), and may number in their hundreds or even thousands (Spilling et al, 1999; Bugoni and Vooren, 2005). The model

discussed in Chapter 3 examines foraging activity in large groups; however as group size increases the model becomes ever more unrealistic. In a situation where foragers do not use public information I, like Valone (1993), propose that an animal may estimate the prey capture success of the group by projecting its own success onto the rest of the group. In other words, it assumes that each forager in the group is experiencing exactly the same success as itself, in effect multiplying its own success by the number of foragers in the group. In large groups this becomes increasingly unlikely. In Chapter 4, I present a modified version of Iwasa et al's (1981) predictor, that removes the bias imposed on patch estimation by large groups. I compare the results obtained using this estimator with those from Chapter 3 for groups not sharing public information. I discuss the usefulness of this model, where it offers an improvement over the original estimator, and also where it has its shortcomings.

Until recently much of the information sharing literature has assumed that animals share information with complete and perfect fidelity. It is often taken as given that animals will have access to accurate information, and that they will be able to obtain this without any form of cost. It is unlikely however, that either of these will occur in nature, and certainly that both will occur together. Numerous psychological studies show that animals have only finite cognitive powers, and by dividing their limited attention between several tasks they reduce their efficiency at each (Rees et al, 1997; Desimone, 1998; Vreven and Blough, 1998; Dukas and Kamil, 2000, 2001). In Chapters 5 and 6 I consider the implications of limited attention in terms of public information use, when foragers must pay a cost for the acquisition of information, and also when information is incomplete or erroneous. In Chapter 5, I develop the information sharing model presented in Chapter 3, and I introduce a cost factor to animals sharing public information. Foragers divide their time between personal foraging and scouting for public information signals given by other foragers. Fernandez-Juridic et al (2004a) point out that many models in the foraging and vigilance literature tend to assume that foraging and scanning are mutually exclusive activities. My model negates this problem. I assume that scouting reduces a forager's ability to notice prey whilst engaged in both activities. The more attention a forager pays towards scouting for public information signals, the lower its personal foraging success will be, and vice versa. I examine the consequences of dividing

attention between two tasks, and discuss ecological situations where public information use (PIU) might remain beneficial.

Where animals observe the behaviour of another, rather than the cues that led to that behaviour, they may be misinformed about the state of the environment (Giraldeau et al, 2002). This may be because the information they receive is biased by the senders physiological and motivational state rather than the receivers. Alternatively it may simply be a genuine error – the animal may have interpreted an innocent movement or sound as a signal. Similarly, true signals may be lost to the environment, and go unnoticed by other foragers. This is especially likely when animals are foraging in areas that have many obstacles (e.g. foliage, rocks) and also when the group contains many individuals or is dispersed over a wide area. In Chapter 6 I examine the effect of public information use (PIU) on foraging success when public information may be erroneous or incomplete. I consider a situation where foragers at any one time stand a chance of accidentally transmitting false signals, informing conspecifics that food has been found when in fact it hasn't, and also where real prey capture signals are not transmitted, so even though prey has been caught, no other group members are made aware of it. I examine the relative effects of both of these errors, and the consequences of information infidelity on foraging groups.

Finally, in Chapter 7 I depart from public information theory and examine a different problem faced by foraging groups. Local enhancement (Poysa, 1992) suggests that animals are likely to be able to find food sources more quickly when in groups than when alone. As groups get larger, food patches will be discovered increasingly quickly. This is a useful simplification for theoretical models. However, in the natural world it is unlikely that the rate of food finding will be proportional to group size. Ruxton (1995a), along with Ruxton and Glaseby (1995), demonstrate that foragers searching for food are often very likely to search parts of the environment already searched by others, and that as group size increases so does the time wasted through re-searching. Additionally, many models assume that once a food source has been located, all group members can arrive there instantaneously, despite being dispersed over a wide area. Again, this is not ecologically realistic. In Chapter 7 I attempt to address these problems. I present a game-theory model that takes into account the spatial considerations of group searching. I argue that there is some

critical distance from a discovered patch, beyond which it is not beneficial for foragers to join it. The cost of travelling means that it may be more profitable to remain searching for another patch, rather than joining one that is far away. Furthermore, in the time it takes for a forager to travel to a patch, it will have been decreased in value by those foragers who were closer and have already arrived there. The patch joining behaviour of animals should thus not only be dependent upon their distance from a patch, but also upon the behaviour of the foragers they are searching with.

In Chapter 8, I summarise my findings from Chapters 3-7 and discuss the applications that they might have within the fields of social foraging and public information theory, and to behavioural ecology in general. I suggest ways in which my work may be extended further, and also how these models could be integrated in future work to give a more complete analysis of how public information and limited attention affects social foraging.

In this thesis I present a series of models, each of which attempts to improve on the current theory by removing unrealistic assumptions and reflecting more closely the natural world. Hopefully the work here will not only offer insights, but also stimulate further questions and opportunities for research in this already exciting and promising field.

CHAPTER 2

PUBLIC INFORMATION THEORY – THE EMPIRICAL EVIDENCE

One of the many reasons that have been proposed to explain why animals live and feed in groups is that of public information use (Clark and Mangel, 1984, 1986; Valone, 1993; Giraldeau and Caraco, 2000; Krause and Ruxton, 2002). Animals that spend time in groups may be able to enhance their own survival or reproductive fitness by obtaining information socially from other individuals, reducing uncertainty about a situation and thus allowing them to make better decisions concerning future behaviour (Valone and Templeton, 2002). For example, an animal may be able to acquire information from another which allows it to learn about the quality of a potential mate (Wiley, 1991; Dugatkin and Godin, 1992), the level of threat posed to it by predators (Treherne and Foster, 1981; Magurran and Higham, 1988; Roberts, 1996), or the availability of food (Ward and Zahavi, 1973; Templeton and Giraldeau, 1996; Wright et al, 2003). Valone and Templeton (2002) suggest that the use of public information may be quite widespread throughout nature. In this chapter I examine some of the existing empirical evidence that surrounds social foraging and information sharing, and that offers support for public information theory. I also discuss the limitations in existing models and where this thesis extends the theory further.

Social foraging and information use.

In terms of foraging, an animal may benefit from the transfer of information in several ways:

1) Travelling as a member of a group may decrease the amount of time and energy that is spent searching for food patches.
2) Animals may be able to obtain food indirectly through observing others, by learning its specific location (area copying) or learning some specific behaviour which will allows them access to food they would not normally have been able to acquire (behaviour copying).
3) Similarly, they may be able to obtain food from others directly, for example by stealing (kleptoparasitism) or scrounging.
4) An animal may also be able to use information by observing the foraging success of others, to assess the quality of food patches, enabling it to estimate the quality of a patch much more accurately than it could do by itself, and thus allocate search time more efficiently.

In the following pages I will look at some of the empirical evidence examining each of these proposed benefits.

Travel time

Many species rely on food resources that are not distributed continuously and evenly throughout the environment, but which are instead clumped into discrete caches, or food patches. Animals feeding in such an environment must travel between these food patches in order to obtain food, moving from one to the next as they are exhausted. It is generally accepted that a group containing several individuals will be able to find food patches more quickly than a forager searching on its own, because there are more animals looking for new patches, and each will benefit by joining another which has found one. This is called local enhancement (Thorpe, 1963 c.f. Poysa 1992). Most theoretical studies tend to assume that this inter-patch travel time is inversely proportional to the number of animals in a group (e.g. Vickery et al, 1991; Ranta et al, 1993; Valone, 1993; Ruxton, 1995b) so that, for example, a group of ten individuals will take $1/10^{th}$ of the time to find a new patch as would a lone forager. Ruxton (1995a) suggests that this is likely to be an unrealistic assumption, because some individuals will probably search areas of the environment that have already been searched by other members of the group. Although the relationship between search time and group size has been studied fairly deeply in theoretical models, (e.g. Caraco, 1981; Clark and Mangel, 1984; 1986; Mangel, 1990; Vickery et al, 1991; Ranta et al, 1993; Valone, 1993; Ruxton, 1995b) only a small number of studies have been carried out to examine this empirically.

Krebs et al (1972) explored the relationship between group size and inter-patch travel time with captive great tits (*Parus major*). In this study, birds were either alone or in groups of two or four individuals, and were allowed to search for food distributed in plastic food cups, fixed to artificial 'trees' constructed from dowel rods. Only one cup per trial contained food and all were filled with chopped paper so that the birds could not identify which cup was profitable and which were not. Results showed that any particular bird was able to find food more quickly when in a group of four, than when in a group of two or when alone. Similarly, birds in pairs were able to find food more quickly than lone birds. One suggestion is that birds searched more intensively for

food when in groups, because of the competition faced over resources, or from fear induced in individuals foraging alone (perhaps due to a perceived increase in predation risk). To examine the possibility of these explanations, the experimenters recorded the search rate of the birds (defined as the number of visits to a new patch) and also the level of crest-raising behaviour performed by birds, which is associated with fear (Blurton Jones, 1968 c.f. Krebs et al, 1972). The experimenters found that birds did not search a significantly greater number of patches in a given time when in groups, than when alone. This eliminates the possibility that food was found faster in groups because birds were searching faster. Although single birds did perform more crest-raising behaviour when alone this was not correlated with the searching rate, and therefore suggests that fear does not affect their ability to find food. The time taken for birds to locate food after the profitable cup had already been discovered by others, was lower than would be expected for each bird if it was searching alone. This suggests that the birds in groups are finding food faster through local enhancement, using information supplied by a successful bird, and are not simply finding it by themselves. The experimenters also note from observations that when food had been discovered by a bird, the other members of the flock immediately stopped their own searching activity to join the successful bird. All these findings are consistent with local enhancement theory.

In another study, Pitcher et al (1982) showed that groups of both goldfish (*Carassius auratus*) and minnows (*Phoximus phoximus*) were able to find food more quickly as the number of individuals in a group increased from 2 to 20 individuals. Food patches consisted of ice cube trays, filled with gravel. In trials, one of the pots in a tray contained a number of goldfish flakes, and this represented a full food patch. Goldfish were given access to three trays placed on the tank substrate, containing a total of 63 pots, while minnows were given one tray vertically suspended in the tank, containing a total of 84 individual pots. During trials one randomly selected pot contained food flakes, and the time in seconds for a focal 'test' fish to find the food patch was recorded in groups of different sizes: goldfish in groups of 2, 4 and 6; minnows in groups of 2, 4, 6, 12 and 20. In experimental trials, as the size of the group increased the time taken for the focal fish to find a food patch decreased, in both species. It is possible that fish in smaller groups took longer to find food because they were more concerned with anti-predator vigilance, thus spending less

time actually searching for food. It was noted that in both species, fish in smaller groups spent less time foraging, probably because they are devoting more time to anti-predator vigilance. However, the experimenters report similar results when examining purely foraging time, as well as total time, so this is unlikely. It was also ruled out that fish devoted more time to searching in groups because of competition between individuals, presumably by providing adequate food to easily feed all fish in a group. All fish were also fed 6 hours prior to experimentation to minimise competition between individuals, and equalise the rates at which they searched.

Pitcher and Magurran (1982) discuss the means by which these fish recognise when food has been discovered by another fish. They suggest that this could be due to behavioural cues - a change from searching behaviour to obvious feeding behaviour. Alternatively, a fish having discovered food may drag it out of the gravel, allowing it to be seen or smelt more easily by others. However, for my purposes, it is not necessarily important to discuss here how individuals in a group recognise a food discovery, only that being a member of a group increases the chance of finding food.

Ekman and Hake(1988), in a similar study with birds showed that pairs of greenfinches (*Carduelis chloris*) found food twice as quickly as lone birds, thus reducing the variance in feeding rate of each bird. Birds were given a choice to forage either alone, or with a partner bird. The environmental set up was similar to that in Krebs et al's (1972) study, with a series of artificial 'trees'. A food patch consisted of four food tubs, at the end of each branch. Food tubs were covered by lids, so that a bird could only find food by opening a tub itself, or watching another bird doing so and joining it. A subject bird was offered two identical aviaries, one of which contained a second partner bird. The subject thus had a choice to either forage alone, or with a partner. The experimenters found that when foraging with a partner, subject birds found food approximately twice as often as when alone. However, this may be a result of the experimental set up, rather than local enhancement per se. To ensure that the birds had access to the same quantity of food, twice as many tubs contained food in the aviary containing a partner bird. In the non-social aviary, 20 seeds were placed in two randomly chosen cups. In the social aviary, 10 seeds were placed in four cups and paired so that each pair contained two full cups were adjacent to each other. The aim of the experiment was to examine the effect of risk-sensitivity

on social foraging behaviour. This experimental set up was necessary to ensure that the subject bird was able to acquire the same amount of food whether it foraged socially or not. The mean number of seeds available to the subject bird therefore remained constant between aviaries, but the likelihood of finding a profitable food cup was higher in the social aviary, by supplying more food cups each of which contained less food. Whether these birds are really finding food more quickly through local enhancement, or simply because it is more widely available in the social aviary, depends upon what they define as a food patch themselves. If each group of four tubs at the end of each branch is considered by the bird to be a food patch then this indicates that the subject bird finding food more quickly in the social aviary, due to local enhancement. But if each tub is considered a food patch by the bird, then the theory breaks down, because there are simply more food patches in the social environment than intended by the experimenters.

Although these studies are valuable, two of the three are unfortunately limited because they only evaluate the effect of group size on the patch finding ability of small groups, where the true nature of any relationship would be impossible to identify. It is also necessary to ensure that the term 'food patch' is adequately defined. The opinion of the experimenters may not be mirrored by that of the species under investigation. Further work taking into account both of these factors would undoubtedly be beneficial to investigate this. However, all three studies examined here indicate that individuals in groups do benefit from finding food more quickly than when alone (in these species, at least), and that this ability increases with group size. We can conclude that animals in groups are using information about the location of food made available by other individuals, but in order to find the true nature of the relationship it would be necessary to extend trials for groups much larger than this.

Area copying

Similar to the benefit of local enhancement mentioned above, is that of fine-level local enhancement (Poysa, 1992; Kendal et al, 2004), or area copying (Barnard and Sibly, 1981). Essentially the same thing, the main difference between these two is that area copying occurs on an individual level, within groups that have already been

formed inside a food patch, while local enhancement occurs over larger areas, and is concerned with groups that are looking for patches in the first place. If we imagine that an animal feeds on the larval parasites inside fruit of a certain type of tree, then it may benefit from being in a group since it will be more likely to find this type of tree (local enhancement). Once the tree has been found, the animal then has to find the fruit - perhaps it has been completely harvested from some branches, or parasites are only found in some fruit - and so will benefit from observing whether others have found a good place or not (area copying). The seemingly trivial difference between local enhancement on these two levels highlights the need to define what a species identifies as a food patch. It emphasises the importance in understanding the ecology of a species before making assumptions about its behaviour and decision processes.

However, numerous studies have shown what is clear area copying behaviour in several species. Barnard and Sibly (1981) demonstrated that house sparrows (*Passer domesticus*) were frequently attracted to the foraging activity of group mates. Small groups of birds (4 or 6 individuals) were left to forage in an arena containing a series of food patches, in the form of a grid. The grid consisted of a series of holes drilled through a sheet of wood, set at 4-inch intervals. During trials 5 food patches, each consisting of 30 holes containing a single mealworm, were distributed around the grid. It was shown that some birds (copiers) were more likely to move towards group members who were searching for prey, than finding their own food. These copiers found more of their prey through copying the same foraging area (within 41cm) of the searching bird, than by searching independently themselves.

A more recent study by Marchetti and Drent (2000) showed that some great tits (*Parus major*) trained to search for food in a specific location were more likely to search in new places when paired with a partner bird that had been trained to search in different locations. These birds were copying their partner despite their own knowledge of prey location. Birds were trained to search for food from one of four types of feeder-tray, which were hung on artificial 'trees' in the experimental arena. The arena was set up so that it was split into two identical halves, each containing two 'trees'. A transparent screen divided the two halves of the arena, so that a subject bird in one side could observe a tutor in the other side, without allowing physical contact. Each tree was fitted with three of each type of feeder. During training for the subject

bird a piece of mealworm was placed, uncovered, in each type of feeder, so that the birds learnt they could acquire food there. Later each feeder also contained a layer of sand, so that birds learnt they had to search in order to find the mealworm. Finally, food availability was restricted to just one type of feeder (green, semi-circular) while the others just contained a layer of sand. Tutors, however, were only ever trained to search in one type of feeder (white, circular); food was only ever available in these so they never expected to find food in any other type of feeder. Food was also never hidden for tutor birds. During experiments, all feeders for the subject bird contained only sand, while tutors were given a piece of mealworm in the white, circular feeders. The subject birds were released into their side of the arena, and were allowed to forage either alone, or with the presence of a tutor bird in the other side of the arena.

Results from this study, and in previous experiments (Verbeek et al, 1994, 1996; Drent and Marchetti, 1999) identified subject birds employing two different foraging tactics: fast explorers and slow explorers. This refers to two suites of behaviours involving differing levels of aggression and curiosity to novel objects, but most of all to patterns of exploration in a new environment. Fast explorers are characterised as being more aggressive, willing to approach novel objects quickly and explore a new environment quickly, but not in depth. They are unwilling to change a specific food-searching pattern once it has been learnt. Slow explorers, on the other hand, are rarely aggressive, take longer to approach novel objects or explore new environments, but are more meticulous in exploring the environment, spending longer in each place.

This study shows that on their own, fast birds did not change their foraging strategy during experimental trials, and continued searching for food in the empty green feeders. Slow birds quickly began to search the other types of feeder. When a tutor bird was present, however, slow birds did not change their behaviour, and continued searching in the empty green feeders, despite the success of tutor birds. Meanwhile fast birds were willing to copy the tutor and quickly began searching in the white feeders. This demonstrates that although area copying behaviour occurs in these birds, it is dependent upon character traits of each individual bird. This work agrees with Krebs et al (1972) who also found that some great tits were more likely to forage in an area - on the same artificial 'tree' and on the same branch - as a bird which could be observed successfully finding food.

Conversely, Pitcher and Magurran (1983) suggest that goldfish (*Carassius auratus*) did not use an area copying strategy when foraging in groups. Shoals of goldfish (containing either 2 or 5 individuals) were established in tanks containing three ice-cube trays, to represent food patches. Each compartment of the trays were filled with gravel, and those containing food had either 1, 4, or 9 flakes of fish food buried in the gravel, representing low, medium and high density food patches. These three patches were arranged in one of two different patterns. After the shoals were trained to recognise the pattern of food profitability in their tank, a single fish from each shoal was swapped with that of another. At this time the patterns of patch profitability were also switched, so that only the swapped fish (informed) was aware of the profitability in the patch they'd been moved to. Immediately after this switch, the informed fish continued to spend a greater proportion of foraging time on the patch of highest density, as would be expected. Despite this, the informed fish also spent a greater time on the poorer patches than before the switch. Results show that the informed fish made a greater number of shorter visits to the high density patch, and also to the patch which had previously been the high density patch for the misinformed fish.

Similarly, after the switch the misinformed fish made a higher number of short visits to both the 'new' and 'old' high density patch. They spent a greater proportion of their foraging time on the lower density patches, because they were unaware of the change in patch profitability, but this sampling behaviour enabled them to locate the new high density patch more quickly. However, for both informed and misinformed fish, sampling only occurred in the shoals of 5. The authors argue that this is not area copying, because this would imply that all fish in the shoal should be on the same patch (the most profitable patch) at the same time - i.e. copying the most successful fish. Rather than this, sampling behaviour was increased to all patches. This was shown by an increased number of visits to the '3rd' patch - the patch which was neither the 'old' or 'new' high density patch. Fish visited this 3rd patch three times more often after the switch than before, without any increase in the duration of visit time. If the fish were copying the location of the most successful fish, there would be no reason to increase sampling in this patch at all, since this was never the most profitable patch, either before or after switching. But this does not necessarily make sense, because the fish could not realistically be expected to find the high density

patch, without first searching at least some of the other patches – including the low density patch. The possibility that fish were willing to spend greater time on less profitable patches due to competition can be ruled out because more food was placed on the high density patch than could be eaten in the given foraging time. Also, in shoals of two, the misinformed fish would be predicted to change its choice of patch more quickly than in groups of five, because it would only have to observe the feeding behaviour of one other individual - i.e. the informed fish. That it didn't do this similarly indicates that area copying does not play a major role in the food acquisition of goldfish. However, the authors do not rule out the possibility that goldfish use ' delayed area copying', i.e. remembering a site visited by another, and using this another time.

Coolen et al (2003) give evidence of similar behaviour in three-spined sticklebacks (*Gasterosteus aculeatus*) and nine-spined sticklebacks (*Pungitius pungitius*). In both species individual fish were significantly more likely to visit sites after they had observed others feeding there, than if they had observed fish not feeding there, but only at a later time. Additionally, nine-spined sticklebacks were also found to be able to correctly identify the richest patches from cues given by feeding fish, by observing their foraging success, thus not only learning about the location of food but also its quality. The experiments were carried out in fish tanks divided into three compartments, divided by transparent partitions. The two outer compartments each contained an upright feeder constructed from a transparent column in which bloodworm would sink down, before it could be eaten by the fish. One side of the feeder was made opaque so that the observer fish, in the central tank, could not see inside it. Three demonstrator fish were placed in each of the outer compartments. The central compartment contained an observer fish, inside half a transparent plastic bottle. For each experiment, one feeder was considered 'rich', and the other 'poor'. The rich feeder offered to or three bloodworm every 90 seconds, for the duration of the experiment. The poor feeder offered either two or three bloodworm after 90 seconds and again after 360 seconds, or only bloodworm juice (the water in which the bloodworm were defrosted). Each side acted as the 'rich' and 'poor' patch an equal number of times. Each experiment ran for 10 minutes, in which the observer would remain in the central compartment, able only to see the activity of the demonstrator fish in the outer compartments, and not the actual allocation of bloodworm. After this

time, the demonstrators were removed, as were the partitions dividing the tank. The observer fish was then left alone in the tank with free access to either of the outer compartments.

The results showed that both three-and nine-spined stickle back were more attracted to the compartment with the 'rich' feeder. This is an example of delayed local enhancement, since the fish were attracted to this site after feeding had finished, and there were no cues present indicating which had been the most profitable site. The experimenters rule out this attraction to the rich feeder as a result of chemical cues in the water, because during experiments the poor feeder also supplied bloodworm, or the water it has been defrosted in. The same olfactory cues would therefore be present in both sides of the tank. Similarly, observer fish could not see which feeder was yielding bloodworm because the side of the feeder facing the observer was opaque. The implication, therefore, is that the observer fish were able to identify the rich patch just by watching the foraging activity of both sets of demonstrator fish during experiments and determining which was most successful.

In accordance with local enhancement theory, Day et al (2001) also report that guppies in large shoals discovered hidden food resources faster than smaller shoals. However, when the fish were faced with leaving the shoal to find food, by swimming through a small hole into an opaque maze, fish in larger shoals took longer than smaller shoals. The authors suggest that this is because guppies prefer to swim in large shoals, and may be prepared to pay some cost, by missing foraging opportunities, in order to maintain this preference. When the maze was constructed with a transparent partition, so that the fish could maintain visual contact with the shoal, they were once again able to find food faster in larger shoals.

Behaviour copying

There is much anecdotal evidence of animals learning novel behaviours from others in order to obtain food they would not normally have had access to. One such example (and quite an impressive one at that) is of the grey squirrel, which in various populations throughout parks in Britain learned to unscrew the caps of fizzy drinks bottles. However, there is also documented scientific evidence of similar behaviour

copying occurring in numerous species. For example the blue tit, *Parus caeruleus*, and great tit, *Parus major*, (Fisher and Hinde, 1949; Hinde and Fisher, 1951 both c.f. Krebs et al, 1972) which are also famous in Britain for having learned how to open the tops of foil milk bottles. Another, (Langen, 1996) showed that white-throated magpie-jays (*Calocitta formosa*) were able to learn how to open a door to obtain food. The magpies learned to do this more quickly when in the presence of tutor (an individual already trained in this behaviour) than with other naive individuals. Lefebvre and Giraldeau (1994) showed that pigeons (*Columba livia*) were able to learn how to peck open stoppered test-tubes containing seeds. Again, their ability to do so increased with the number of demonstrators. In another study, Hosey et al, (1997) reported that wild-roaming ring-tailed lemurs (*Lemur catta*) in a social group learned to suck water from their saturated tails after dipping them into water. Others not performing the behaviour were seen watching those who were, and sometimes sucking the water from the tails of others rather than their own.

This type of learning is not confined to birds and mammals. Young perch (*Perca fluviatilis*) were shown to suffer lowered food intake rates whilst visiting a novel food source in the absence of a tutor, in comparison to those in the presence of a tutor (Magnhagen and Staffen, 2003). Juvenile fish, with no experience of the novel food source, lost body mass when feeding alone, but those in the presence of experienced tutors had a positive growth rate. Wild-caught fry were reared in one of two treatment groups: one half (untrained) in a barren fibreglass tank, while the other half (trained) were reared in an enriched tank containing gravel substrate and artificial vegetation. The experiment was carried out in an enriched environment similar to that of the trained fish. Both types were fed red chironomid larvae (bloodworm). Demonstrator fish, wild-caught from the same lake as the fry, but at a later date, were raised in a similar enriched environment and also fed on bloodworm larvae, but by the time the experiment took place they were also trained to accept a novel, dry food. During the experiment these fish were put into groups of four: 2 untrained fish with 2 demonstrators; 2 trained fish with 2 demonstrators; 4 untrained fish; 4 trained fish. Each was introduced to the new dry food type, in the enriched environment.

The body mass of each individual fish was measured on the start date of the experiment, and recorded weekly over the following three weeks. At the beginning

of the experiment, although body mass of the demonstrator fish was significantly greater than the test fish, there was no significant difference between the body mass of the four experimental groups. Of the four test groups, only the untrained fish paired with demonstrators saw a positive increase in body mass during the first growth period (i.e. between the first and second recording). The growth rate of untrained/demonstrator fish was also not significantly different from that of a fifth group, consisting solely of demonstrator fish. These results suggest that inexperienced (untrained) fish, were able to benefit via social learning, aided by the food-finding behaviour of experienced demonstrators. Fish previously trained in the enriched environment, in which food was delivered in a different way (trained/demonstrator groups) were perhaps slower to respond to the novel food source because this conflicted with what they had previously learnt. The untrained fish, on the other hand, which were not experienced in the enriched environment, were able to learn more quickly when paired with demonstrators, because the whole environment was novel and there were no prior expectations.

This work is supported by a number of similar studies with other species of fish: guppys, *Poecilia reticulata* (Laland and Williams, 1997), Atlantic salmon, *Salmo salar,* L (Brown and Laland, 2002) and trout, *Salmo trutta* (Sundstrom and Johnsson, 2001). Similar studies have similarly shown that animals may also use demonstrator individuals as models to determine which foods are safe to eat (Benz, 1993; Galef and Whiskin,1992; Sherwin et al, 2001;) and to find specific routes to a food source (Laland and Williams, 1997). Interestingly, both fish (Bates and Chappell, 2002) and dogs (Pongracz et al, 2003) have been shown to do this even if they were following an individual that was trained to use the most costly route. This strongly suggests that social information of this kind may be considered as highly valuable by some animals.

Lefebvre and Giraldeau (1996) suggest that the comparison of social learning ability between different species is unnecessary and inappropriate, and that animals of a social species should show a generally enhanced ability to learn novel skills when in groups then when alone. This was tested by Templeton et al (1999) using two species of corvid: the pinyon jay (*Gymnorhinus cyanocephalus*), which is a highly social species, forming very large cohesive groups, and the Clark's nutcracker (*Nucifraga*

columbina), which is far less social, mostly living in pairs, or small, uncohesive groups of only a few individuals. Both species share similar habitats and foraging ecologies, and are close taxonomically.

Six wild caught nutcrackers, and six wild caught pinyon jays were used as subject birds. One more of each species, also wild caught, were trained as demonstrators. All birds were housed separately. The birds were subject to two tests: a motor task and a discrimination task, to avoid inter-specific differences in learning. The motor task consisted of a single well drilled into a block of wood, and covered with a lid. Hidden inside the well was a single pine seed. In order to obtain the seed, the birds had to first peck off the lid covering the well. The discrimination task consisted of two wells, each covered with a lid. One lid was coloured purple with a green square, and the other green with a purple square. For both tasks 30g weights were taped to the underside of the lid to prevent them being knocked off accidentally. During trials, subject and demonstrator birds were kept in adjacent cages of equal size. Each cage was fitted with either one well with a white lid, or two wells with the two different coloured lids, depending upon the task. Subject birds of both species were split up into two groups. One group performed the motor task individually and the discrimination task socially, while the other performed the discrimination task individually and the motor task socially.

For the motor trials, demonstrator birds (which had been previously trained to peck off the white lid covering the well) were offered the apparatus containing the food well. They performed one demonstration, removing the lid and eating the pine seed. Following this demonstration the apparatus was removed and a similar apparatus was offered to the subject bird. Trials continued like this until the subject bird removed the lid for five trials in a row, or until 40 trials had passed. Experimental set-up for the discrimination task was similar to that of the motor trials, except that both demonstrator and subject birds were offered two food wells, only one of which contained a pine seed. The demonstrator was able to identify the well containing food because it was marked with a black sticker (this was not visible to the subject bird). By this time all subject birds had learned how to remove the lids from the wells. In a trial, eight presentations of the feeding apparatus was made to the demonstrator, followed by four presentations of similar feeding apparatus to the

subject bird. Subjects also performed four individual discrimination trials each day. These were the same as for the social discrimination trials, except that the demonstrator bird was hidden from view, and thus could not indicate which lid pattern offered food. As before, trials continued until a bird had successfully obtained food for five trials in a row, or until 40 trials had occurred. Collected data were pooled for analysis.

Results showed that the pinyon jays were better at the learning tasks when in pairs then when alone, whilst nutcrackers were better at learning when alone. All six of the subject jays learned to complete the motor task, obtaining food, when in the social condition, whereas only 2 did so in the individual condition. Conversely, 5 of the 6 nutcrackers obtained food in the individual condition but only 2 did this in the social condition. Pinyon jays also learned significantly more quickly during the social condition than in the individual condition, while nutcrackers learnt slightly (but not significantly) more quickly in the individual condition. The data from the two tasks were also analysed separately. The results just for the motor task did not differ from when pooled. However, the discrimination task found no significant difference between species when analysed separately. Pinyon jays learned how to obtain food in fewer trials during social trials than did the nutcrackers, but this was not significant. They also took significantly longer during individual trials than the nutcrackers.

The implication from these results is that the pinyon jay, a highly social species, learns novel skills more quickly when in social groups, than when alone. Nutcrackers on the other hand, which are less social than pinyon jays, did not differ in their learning ability when they were alone or in groups. This supports Lefebvre and Giraldeau's (1996) hypothesis that social learning may be an adaptation to sociality, and that comparing the abilities of different species is pointless, without bearing in mind the social dynamics of the species in question. A further inference from these results is that although animals may pay attention to the behaviour of a demonstrator animal, they may not pay attention to specific details of the behaviour performed. Although the pinyon jays learned to copy the demonstrator in the motor task, thus obtaining food by opening the lid covering the food well, they did not learn to identify which of the two wells contained food by the lid pattern in the discrimination trials. Animals in large groups may find it difficult to follow the specific details of

several individuals performing the same behaviour, but with slight variation between them. This could easily lead to confusion over which behaviour they should perform, and may be more harmful than helpful. Instead, roughly mimicking a behaviour performed by those same individuals may increase the chances of the animal developing its own similar method of obtaining food. Within this experiment, it was noted that there was some variation between individuals in opening the food well during the motor task, although this occurred with the nutcrackers rather than the jays.

However, simply copying the behaviour of an 'informed' individual, no matter how vaguely, may also have an adverse effect on foragers, and similarly on the results of this study. Although copying the demonstrator bird during social motor trials increased the likelihood of obtaining food in both species, during individual trials when the demonstrator bird was present but was non-performing, none of the pinyon jays did anything either. They copied the demonstrator and obtained no food as a result. Templeton et al (1999) suggest that the experiment might be improved by not using a non-performing demonstrator during individual learning tasks, if this encourages the subjects to do nothing. Alternatively, during trials subject birds could be presented with the task alone, or if a demonstrator need be present to maintain sociality, perhaps they should be given an entirely different behaviour clearly not linked with feeding.

Kleptoparasitism

Kleptoparasitism, defined by Giraldeau and Caraco (2000) as 'parasitically exploiting food that another forager's efforts have made available', has been the subject of considerable study, both theoretical (e.g. Barnard and Sibly, 1981; Vickery et al, 1991; Caraco and Giraldeau, 1991; Koops and Giraldeau, 1996; Ranta et al, 1996; Broom and Ruxton, 1998, 2003) and empirical (e. g. Brockman and Barnard, 1979; Barnard and Sibly, 1981; Packer and Ruttan, 1988; Ens et al, 1990; Koops and Giraldeau, 1996; Templeton and Giraldeau, 1996; Goss-Custard et al, 1998; Smith et al, 1999; Coolen, 2002; Galvan, 2003). Using the definition above, there are several types of kleptoparasitism that can be considered. (Giraldeau and Caraco, 2000).

The first, and perhaps the most commonly studied example of kleptoparasitism, is 'stealing'. This definition implies some form of aggressive interaction between individuals, or the threat of aggression, in order to obtain food from another individual (Giraldeau and Caraco, 2000). Stealing is therefore most likely to occur when the cost of finding food is very high, and when it cannot be shared. It may also be intra- or inter-specific. Ens et al (1990) showed that curlews (*Numenius arquata*) feeding on mudflats tended to steal food from other curlews, which were subordinate to themselves. They in turn were targets of stealing by gulls. Galvan (2003) reported, similarly, that lesser black-backed gulls (*Larus fuscus*) preferred to steel food from other gulls equal in age, or younger than themselves. The success of these attacks increased with the age of the robber, and decreased with the age of the victim. Conversely, Goss-Custard et al (1998) found that juvenile oystercatchers (*Haematopus ostralegus*) stole mussels mainly from older birds. As the gulls grew older they stole fewer mussels and relied more on mussels obtained personally through foraging. Goss-Custard et al (1998) suggest that this occurs because younger birds are less efficient at finding mussels themselves, and so can maximise feeding rates by stealing when they are young. As they grow older, they become more efficient at finding mussels, and it is less profitable to steal mussels from other birds because they usually only acquire mussels which have been partly eaten by the victim bird. Templeton and Giraldeau (1995a) also showed that starlings (*Sturnus vulgaris*) were willing to steal food from a subordinate partner bird, using physical force or vocalisations to displace them from a food patch when they thought food was present.

The second example of kleptoparasitism, referred to by Giraldeau and Caraco (2000) as scramble kleptoparasitism, is similar to stealing but does not involve aggression between individuals. Here the food source may be shared by more than one animal, which are simply attracted to a source discovered by another. I have considered several examples of this type of exploitation earlier, in the sections looking at local enhancement and area copying.

The third example is stealth kleptoparasitism (Giraldeau and Caraco, 2000). Here, animals avoid any interaction with the individual initially finding the food source. For example an individual may take food which has been dropped by another, or which has been temporarily or permanently abandoned by another. This has also

been termed pilfering and is perhaps most likely to occur in species which hoard food caches (Vander Wall and Jenkins, 2003). Several studies show that pilfering occurs in squirrels (Wauters et al, 2002), chipmunks (Elliot 1978, c. f. Giraldeau and Caraco, 2000), kangaroo rats (Daly et al, 1992), scrub jays (Emery and Clayton, 2001) and arctic foxes (Samelius and Alisauskaus, 2000). However, pilfering as such does not necessarily rely on information that has been acquired socially, since food caches may be raided by animals finding them by chance, rather than specifically remembering their location from past interactions with the owner of the cache.

Alternatively animals may scavenge food scraps from others. This is seen in many species, for example vultures are well known to scavenge food scraps from the carcass of animals killed by larger carnivores, but this behaviour also occurs in other birds (Travaini et al, 1998). Similar behaviour is seen in hyena (Skinner et al, 1995), wolves (Wilmers et al, 2003) and bears (Quinn and Buck, 2000). A recent study by Vucetich et al (2003) examined the effect that scavenging ravens has on the social dynamics of wolf packs. Over a 27 year period the authors collected data from Isle National Park, USA, which is a single-prey/single-predator system between moose (*Alces alces*) and wolf (*Canis lupus*). This allowed an accurate record of the per capita prey capture rate (moose per wolf) in each wolf pack, and the abundance of moose available in each pack territory. Calculations of energetics and metabolic rates show that adult wolves can maximise their foraging rates by hunting in pairs. In groups larger than this, foraging rates are lower than that when foraging alone. However, the median pack size was observed to be 5 individuals.

Wolves were forming packs consistently larger than predicted, and according to the calculations each individual was worse off than if it were not in a pack at all. But this ignores the effect of scavenging on wolf-kill carcasses by ravens (*Corvus corax*). Ravens are the most significant scavengers of wolf kills, and during this study period between 5 and 15 ravens were observed on almost every single wolf-kill. Calculations from observations showed that ravens remove between 2 and 20kg of food from a carcass per day. The authors suggest that this is the reason why wolf packs (in Isle National Park, at least) are consistently higher than predicted by prey rate-maximisation, or risk-minimisation theory. Wolves can counter this by hunting in larger packs, and concentrating on large prey (moose). Although scavengers

consume more of each carcass if prey are large, wolves experience considerably higher prey intake rates than if they switch to hunting smaller prey (deer), especially since hunting, which is extremely costly in terms of energy and risk of injury, would have to be carried more frequently. This study is not only a good example of a typical kleptoparasitic relationship, but also the effect that such behaviour can have on the activities and social behaviour of another species.

Patch estimation

Public information, as defined by Valone (1989), is information obtained vicariously by observing the sampling success of other individuals. This differs from the other types of socially acquired information talked about here, which simply leads to an animal learning about how to gain some food source, because public information is used to reduce environmental uncertainty and benefit future behavioural decisions. Public information specifically concerns the estimation of the quality of the food source (Valone, 1989; Valone and Templeton, 2002). In its original context, Valone (1989) examines the use of public information by group foragers in depleting, contagiously distributed food patches. Such foragers use public information to more accurately assess the depleting quality of each food patch as they feed there, aiding their decision of when to quit foraging in each patch and move to another. However, public information may also be used more extensively throughout nature, in the assessment of environmental resources other than food patches (Valone and Templeton, 2002). Indeed, there is empirical, as well as theoretical evidence to suggest that animals use public information for the assessment of breeding patch quality (Cadiou et al, 1994; Schjorring et al, 1999; Brown et al, 2000; Doligez et al 2002), the quality of potential opponents and competitors (Oliviera et al, 1998; Johnsson and Akerman, 1998; Peake at al, 2001; MacGregor et al, 2001; Johnstone, 2001) and for the assessment of the quality of potential mates (Dugatkin and Godin, 1992, 1993; Nordell and Valone, 1998; Otter et al, 1999; Menill et al, 2003; Herb et al, 2003).

One example of this is given by Doligez et al (2002). They demonstrated that flocks of collared flycatcher (*Ficedula albicollis*) are able to use public information to estimate the quality of breeding habitats. The authors manipulated the breeding

success of wild flycatcher, by moving a number of week-old nestling birds between nest sites. By doing so they established areas in which the mean number of fledglings per breeding pair either increased, decreased or remained unchanged. They then recorded the movements of birds between sites, to follow the emigration and immigration of birds from year to year. Rates of immigration and emigration were recorded for different age classes, and for both male and female birds. The authors predicted that if flycatchers were able to use public information to estimate breeding habitat quality, then the number of birds in sites which had been artificially improved in quality, with the addition of week old nestling birds, should increase from one year to the next. Similarly, in areas which had the mean number of fledglings decreased, by the removal of nestlings, the emigration rate should be higher from one year to the next.

The outcome of these experimental conditions was that the mean number of fledglings per breeding pair of flycatchers increased, in areas with artificially enhanced breeding success, while this decreased in areas with artificially decreased breeding success. The control plots, which were left unchanged, showed no change in the number of fledglings from one year to the next. Further, the authors also recorded a change in the body condition of young birds at fledgling, between treatment groups. This comes as a direct result of the experimental manipulation due to increased competition between young birds for available resources. In the plot in which the mean number of fledgling birds were artificially increased, the mean body condition of young at fledgling decreased, while this increased in the plots containing smaller broods. In one of the two control plots, the body condition of fledglings increased, while in the other it decreased.

The results show that the emigration rates of flycatchers between plots were higher in both of the experimentally manipulated test groups than the control groups. But there was no difference in emigration rates between the groups which had been manipulated, nor between the two control groups. The implication from this is that the flycatchers were using both the number of fledglings and also the quality of fledgling body condition as sources of public information, to assess breeding patch quality. If only fledgling number were used as a cue to habitat quality then we should expect to see higher emigration rates from the plots which contained experimentally

decreased brood sizes only, because each pair on average fledged fewer chicks. The emigration rates in experimentally increased broods should be low, because more chicks would be fledged. On the other hand, if flycatchers were using body condition only, then this should be reversed so that emigration would be higher in experimentally increased groups because body condition of fledglings was inferior due to increased competition between young. Similarly, emigration should be higher in experimentally decreased plots since mean body condition was higher. That both experimentally increased and decreased plots showed high emigration rates implies that the birds were trying to move away from both experimentally manipulated sites, presumably because they considered both as low quality – i.e. they were using both the number of fledglings and the quality of fledglings as indicators of habitat quality.

Studies by other authors similarly show that cormorants (Schjorring et al, 1999), kittiwakes (Cadiou et al, 1994) and cliff swallows (Brown et al, 2000) base their choice of breeding site upon the success of other birds on particular sites. New breeders assessing the quality of breeding sites (prospecting) by monitoring the breeding success of other birds during one year, chose higher quality nest sites and were more successful as breeders themselves the following year. Meanwhile, animals have also been shown to use public information obtained through observing, or interacting with other individuals to assess the quality of potential competitors or mates. Oliveira et al (1998) demonstrated that male siamese fighting fish (*Betta splendens*) use information gained through observing interactions between conspecifics, to assess the quality of other males. The experiments were carried out using tanks, divided into three main compartments by one-way mirrors. A subject fish was placed in the central compartment, and two non-subject fish in each end compartment, separated by opaque partitions with one in each sub-compartment. During experiments the partition separating fish in one of the end compartments was replaced with a transparent one, while the other was left in place. Thus, the subject fish could see both fish in each end sub-compartment without being seen itself, while the fish in one end compartment could see and interact with each other, but those in the other could not. The experimenters recorded the amount of time the subject fish spent within a 5 cm area of each of the end compartments, the amount of time spent within the same 5 cm area facing conspecifics, and the amount of time facing conspecifics generally.

Results showed that the subject fish spent significantly more time at the end of the tank next to the compartment in which the non-subjects were able to interact with each other (through the opaque partition). Since there this side of the tank was randomised between fish, and there was no previous preference, this suggests that the subject fish was attracted to fish interacting with each other.

To test whether the subject fish were able to use the information acquired through watching these interactions, the same experiment was performed but in each end compartment there was a clear winner and loser to the interactions. If the subject fish pays attention to the interactions, and uses this information in an assessment of competitor quality, then they should be more willing to approach the loser in the compartment with a transparent partition than they would the winner. In the compartment with an opaque partition, there should be no preference since the 'winner' and 'loser' do not actually interact. The time it takes the subject to approach each conspecific was used as an indicator of their willingness to engage in a fight with them. The experimenters report that the subject fish did exactly this. They took longer to approach the winners than the losers in the transparent-partition compartment, while there was no difference in the time to approach either winner of loser in the opaque-partition compartment. These results therefore suggest that subject fish were more willing to fight individuals seen to lose fights previously, than those observed to win. Fish were matched for size, so this is not likely to be due to a difference in size between subject and either of the conspecifics, and there was no significant difference between the brightness of body colour, or competitive ability of these fish.

In a similar experiment, albeit with a different methodology, Johnsson and Akerman (1998) showed that rainbow trout, *Oncorhynchus mykiss*, also assess the quality of potential competitors by observing interactions between conspecifics. Trout were more aggressive towards conspecifics they had seen lose consests with others, and were less aggressive towards those they had observed winning these interactions. Trout paired with unfamiliar fish, whom they hadn't encountered in previous interactions, maintained relatively high levels of aggression regardless of whether their partner had won or lost its previous contests. Further support for the use of

public information in competitor assessment has also been found in great tits (Peake at al, 2001) and black-backed chickadees (Mennill and Ratcliffe, 2004).
By the same token, animals may also use public information that may help them to better judge the quality of potential mates. Herb et al (2003) showed that female Siamese fighting fish (*Betta splendens*) preferred males they had observed to win contests with other males. By contrast naive females, unaware of the contests, have no preference for either male. Meanwhile, Otter et al (1999) demonstrated that female great tits (*Parus major*) eavesdrop on male song contests, and were more likely to visit males deemed dominant from these interactions. Interestingly, the results of the former study (Herb et al, 2003) suggest that males losing contests prefer to court naive females, than females that were aware of their defeat. Winner males had no preference between naive and eavesdropping females. This implies that males are able to modify their courtship behaviour, directing it preferentially towards the female most likely to mate with him, not only assessing their own quality, but also the most likely female response to it – in a way, counter-eavesdropping.

Animals feeding in spatially clumped and finite food patches experience a decrease in their capture rate in each patch they visit, as they harvest food from it. There is therefore some point at which a forager can do better by travelling to another patch than by staying and searching for the ever-diminishing amount of prey in the present patch. When prey is cryptic or hidden, a forager cannot know the quality of each patch and must estimate its quality in order to decide when it should leave and move to another patch. Provided the forager knows the distribution of prey throughout the environment an animal can do this using the information it gains from sampling as it forages (Charnov, 1976; Cowie, 1977; Pulliam, 1980; Iwasa et al, 1981; Green, 1988; Alonso et al, 1995; Valone and Brown, 1989; Cuthill et al, 1990; Livoreil and Giraldeau, 1997; Gils et al, 2003). Animals feeding in groups, on the other hand, may also have access to an extra source of information of the decreasing patch quality - the sampling information of other foragers in the group. Animals foraging in groups should be able to form more accurate estimates of decreasing patch quality if they use information of their own foraging success and also that of other group members, than if they simply used their own (Clark and Mangel, 1984, 1986; Valone, 1989, 1993; Valone and Giraldeau, 1993; Ruxton, 1995a). This is the correct definition of the term 'public information use' (Valone 1989; Valone and Templeton, 2002). Animals

using public information in this way should be able to utilise food patches more efficiently since they should be able to quit patches closer to the threshold level of prey, wasting less time in poor patches and spending a longer time in more profitable patches.

One way animals could gain knowledge of the foraging success of others is if a signal is given by a forager each time a prey item is found. This could be achieved either as a deliberate signal, for example a specific food-finding vocalisation. Elgar (1986a,b) reported that house sparrows (*Passer domesticus*) give chirrup calls when they have located a food source which is divisible, even though the caller often received a smaller share of the food than if it were to feed alone. Benz (1993) suggested that golden lion tamarins (*Leontopithecus rosalia*) make vocalisations referring to their individual preference of discovered food items. Meanwhile, Bugnyar et al (2001) think that food yells given by ravens (*Corvus corax*) are intended to supply not only information as to the location of the food source, but also its quality.

Alternatively such a signal could occur as an intrinsic part of feeding, such as simply seeing another forager handling prey, or the head position of the forager. Coolen et al (2001) demonstrated that the head position of ground-feeding birds can be used as a reliable indicator as to whether a bird has found food or not. In this study, 25 spice finches (*Lonchura punctulata*) were split into five groups, each containing five individuals. Experiments were carried out in an indoor aviary, in which had been placed a plywood grid, drilled with 198 food wells. During experiments, 20 randomly selected food wells were each filled with 10 millet seed. Each flock was introduced to the aviary and allowed to forage on the grid, while an observer recorded behaviour of a focal bird. The observer recorded the following behaviours: head up, head down, stationary, hopping, finding (feeding from an unoccupied food well), joining (feeding from an occupied food well), and also any other behaviours performed. Each flock was allowed to feed until all patches had been depleted, the focal bird had left the grid for more than one minute, or a maximum of 5 minutes had passed. Each flock was tested five times each day, over a period of three days, with a 20 minute interval between trials. The mean length of time spent performing each behaviour was calculated over the three days, and an analysis of covariance was used

to determine how strongly each behaviour was associated with the finding and joining behaviours.

The results obtained from this data showed that the finding and joining behaviour of spice finches was strongly associated with the position of their head while hopping. Birds hopping with their head down were significantly more likely to be feeding (finding its own food). No other behaviours were found to be linked with feeding. Conversely, birds spending more time hopping with their heads up, and less time with their heads down, were significantly more likely to be joining others which had previously found food. The authors interpreted this as an indication that birds scanning for the foraging activities of others (head up) were less likely to be feeding themselves.

In a further experiment, Coolen et al (2001) altered the spatial distribution of food resources within the foraging grid. By creating a fewer number of rich patches, joiner birds would see a higher share of each patch that has been discovered. Under these circumstances, it was predicted that a higher proportion of a population would be joiners, scrounging from the finds of other individuals, than searching for food themselves (Vickery et al, 1991). Thus, the authors predicted that if head position is an accurate indicator of whether a bird is feeding, they should spend a higher proportion of their time hopping with their head up, and less time hopping with their head down. Similarly, when food resources are distributed over a greater number of low value patches, scrounging is less profitable, and so the authors predicted that the birds would spend a smaller proportion of time hopping with their head up, and a greater time hopping with their head down.

Three flocks of seven spice finches were examined, using the same experimental protocol as before, but with two variations: in one series of trials, 40 random food wells were filled with 5 millet seed, and in a second series of trials 10 randomly selected wells were filled with 20 seeds. The results obtained during these trials showed that the frequency of birds hopping with their head up changed as in relation to the distribution of prey resources, as predicted by Vickery et al's (1991) producer-scrounger model. When the share of food obtained by joiners increased, the proportion of birds hopping with their head up also increased. The authors conclude

that the head position of spice finches can be used as an indicator of whether a bird is feeding or looking for scrounging opportunities.

Earlier studies with dark-eyed juncos (*Junco hyemalis*) and American tree sparrows (*Spiza arborea*) similarly demonstrate that the head-up position may also be associated with anti-predator vigilance, or some other type of scanning (Lima, 1994), and other activities not associated directly with feeding.

Several theoretical studies have highlighted the benefits of public information use, in terms of patch estimation for group foragers (Clark and Mangel, 1984, 1986; Valone, 1993; Ruxton, 1995a), but there is also some empirical evidence supporting this theory. Fernandez-Juridic and Kacelnik (2004) demonstrated that starlings (*Sturnus vulgaris*) altered their foraging behaviour in response to the behaviour of surrounding birds. Individual birds were placed in three adjacent cages, simulating a small flock but preventing interference between birds. Each of the starlings in the end cages were considered as 'senders' while the bird in the middle cage was referred to as the 'receiver'. The foraging conditions of the senders were manipulated so that they either contained one of three states: enhanced-feeding (E), no-foraging (Z), and natural-foraging (N). The bird in the central cage experienced natural foraging conditions at all times – feeding from the turf through the bottomless cage floor. Where enhanced, mealworms were buried in a number of places around the turf substrate. For no-foraging a sheet of wood over the substrate to prevent probing at all.

For each combination of E, Z and N the scanning and foraging behaviour of the sender and receiver bird was recorded and examined. Not surprisingly, senders increased foraging activity in enhanced conditions, compared with natural conditions. Both the probing rate and prey intake rate were higher than when food was at normal expected levels. Receivers also altered their behaviour in response to the sender's conditions. Probing rate increased in enhanced conditions and decreased in no-foraging conditions, in comparison with natural conditions. Since their own foraging state was not manipulated, this suggests that the receivers were responding to the behaviour of the senders – probing more frequently when the sender did so, and less frequently when the sender did not. Receivers were also noted to spend more time

scanning (i.e. watching) senders in enhanced conditions, and also in no-foraging conditions.

Templeton and Giraldeau (1995a) reported that foraging starlings were able to use information made available to them by partner birds to indicate whether food was available in a food tub or not, although this information occurred in the form of colour cues, rather than the actual foraging success of a partner. Starlings were presented with food patches made from cardboard cylinders, divided into two compartments. These were attached to wooden supports by one end of the cylinder, closing it off. The other end was fitted with a lid, held closed by a paper seal. To obtain food birds had to break through the seal, thus opening the lid. This allowed birds access to the first 'information' compartment, containing either a piece of yellow or black coloured paper. Birds could then break another seal inside the cylinder into the second 'food' compartment.

During training, birds were divided into three treatment groups, termed 'black', 'yellow' and 'control'. Birds in the black group were trained to learn that when a piece of black paper was present in the information compartment then food was available in the food compartment. Birds in the yellow group were trained to expect food when a piece of yellow paper was present. Birds in the control group learned that neither black or yellow paper signified the presence of food; each colour was present 50% of the time. During experimental trials eighteen such containers were present in an arena, nine of which contained food, while the other nine remained empty. Subject birds were introduced into the arena, in the presence of a specially trained partner bird. The partner was trained to check each patch, irrespective of the colour of the piece of paper inside the information compartment. Trials were carried out in three experimental environments: 'informing', 'uninforming' and 'misinforming'. During informing trials, the colour of the paper in the information compartment remained the same as during training sessions, providing birds with correct information about the presence of food in each patch. During uninforming trials the colour cues were removed, so birds had no cue as to the presence of food. Lastly, during misinforming trials the colour cues were reversed, so that they indicated the opposite of that during training; i.e. if black indicated food during training, there was no food to be found

during misinforming trials. These cues remained meaningless to birds in the control group.

When the partner bird opened a patch, thus revealing the paper colour cue, fifteen of the eighteen subject birds were willing to scrounge from the partner bird if they thought food was present. Moreover, when the colour cues provided correct information about the presence of food, subject birds scrounged from a higher number of profitable patches than did control birds (which had been trained to ignore such cues). They also successfully avoided empty food patches. Similarly, when the colour cues were misleading about the presence of food, subject birds scrounged from a higher number of empty patches than the control birds. These findings suggest that these starlings were using foraging cues, made available by another bird, whether this was foraging success, or lack of it, to indicate the quality of a food patch, and modified its their behaviour accordingly.

Templeton and Giraldeau (1995a) suggest themselves that the use of colour cues in this way cannot truly be considered as public information use, because it relies on environmental rather than behavioural stimuli. But that being said, the cues were not available to the subject bird until after the partner had 'opened' the patch. In a further experiment, Templeton and Giraldeau (1996) demonstrated that starlings were also able to utilise the foraging success of a partner bird as a source of public information. This experiment was carried out in two parts. In the first, the experimental arena contained two pieces of foam, separated by a wooden divider, and drilled with a series of 30 holes, in a 2x15 array. Covering each foam sheet was a strip of latex, with slits cut over each of the holes. Each piece of foam represented a food patch, and each hole could potentially contain a piece of food. A bird could only assess whether food was in each hole by stretching open the slit in the latex sheet covering it. A subject bird was allowed to forage in each of three conditions: alone, paired with a 'low information' or paired with a 'high information' partner. 'Low information' partners were trained to expect food in only three marked holes, thus searching only a small number of holes (which they could easily identify), and providing little sample information to the subject. 'High information' partners were trained to expect food in only one random unmarked hole, and so searched many holes providing much sample information.

During experimental trials both patches were empty. If starlings were able to use the sampling behaviour of another bird to indicate the quality of a food patch, then the subject would be expected to leave patches after searching fewer holes when paired with the 'low information' partner than when alone. This is because the 'low information' partner is supplying information suggesting that the patch is of low quality. The subject bird can use both its own lack of foraging success, as well as that of its partner, to conclude that the patch is poor in quality. When paired with the 'high information' partner subject birds should be expected to search even fewer holes before it leaves, because the partner is demonstrating that the patch is of even lower quality, since it is sampling many holes and still not finding any food.

The second part of this experiment differed in only one way from the first: in the first the holes punched into the foam sheets were arrangement in a 2x15 array; in the second part of the experiment the holes were arranged in a 6x5 array. Thus, the difference between the two is the ease with which both personal and public information could be acquired. In the first arrangement the partner bird was often not in view of the subject bird, because they were at different points along the row of holes, making it more difficult to observe the partner bird. Also, since the holes were essentially arranged in a straight line in the first part of the experiment, the subject was able to move over the patch systematically, and could thus be much more confident of the reliability of its personal patch sampling information. Using the 6x5 grid it was not only much simpler for the subject bird to observe the foraging success of its partner, but should also be much more likely that the subject would search in a random manner, thus re-probing some holes and finding it more difficult to accurately assess the true patch quality.

In the first part of this experiment, there was no significant difference between the number of holes sampled before patch quitting, whether the bird was alone, or when paired with a 'low' or 'high' information partner. Thus, there is no evidence for the use of public information use in the first part of the experiment, and birds were estimating patch quality purely upon their own foraging success. However, in the second part of the experiment, when patches were arranged in a 6x5 grid, subject birds sampled significantly fewer holes when paired with a 'low information' partner than when alone, and fewer holes still when paired with a 'high information' partner.

These results are consistent with the author's predictions, and support the use of public information. The authors conclude that starlings may use public information to supplement their own personal sampling information, but only under certain circumstances. When public information is easy to acquire, without sacrificing a forager's own sampling, starlings are willing to use the foraging success of others to complement their own patch sampling. But when it is more costly to acquire this information, or when personal sampling is more reliable, they prefer to rely on their own sampling, ignoring that of their partner.

One other possible explanation for the results obtained in the second experiment is that the subject bird considered the 'high information' partner bird to be a stronger competitor than the 'low information' partner, because it sampled more holes. The authors reject this explanation for two important reasons. Firstly, if the 'high information' partner was considered as a competitor, it would also have been considered a competitor in the first experiment, and the subject should have similarly spent less time foraging on a patch than when paired with the 'low information' partner during the first experiment also. Secondly, if the 'high information' partner was considered a competitor, the subject bird would be expected to forage more vigorously, in order to obtain as much food as possible before the 'competitor' did so. This did not happen, but rather the subject bird probed less frequently, suggesting that they were spending more time observing the activity of the partner bird, rather than competing against it. The authors also report that, although both the patches were intended to be empty during experimental trials, on one trial a piece of mynah pellet was accidentally left in one of the holes in the partner bird's patch. When the partner bird discovered this, the subject immediately rushed over to it, checked the same hole, and others around it. Although anecdotal, this example suggests that the subject was paying attention to the foraging success of the partner and modifying its behaviour accordingly.

In a similar study to this, Smith et al (1999) examined whether red crossbills (*Loxia curvirostra*) were better able to assess the quality of food patches when in pairs or groups of three, than when alone. In the experiments, two artificial trees were placed in an aviary with a mesh divider down the middle, so that half of each tree was in each side of the aviary. Attached to the limbs of the trees were open lodgepole

pinecones, so that a total of 40 pinecones were mounted on each half of the tree. During trials, only one of the trees offered food, and the other was empty. Four cones of the profitable tree contained three pine seeds. Subject crossbills were allowed to feed in one side of the aviary either alone (with a non-foraging partner in the other side of the aviary), in pairs, or in groups of three (paired with one of two foraging partners on the other side of the aviary respectively). When in groups of three, the amount of food made available to the two partner birds was doubled, so that on average each bird had access to the same amount of food. Subject birds fed in a series of trials, and the number of cones sampled on each tree was recorded, as was the amount of time spent on each tree.

If crossbills are able to use public information, the authors predict that the subject bird would spend less time foraging on the empty tree when in pairs or groups of three, and would search a smaller number of pinecones, since they would also be using the prey capture success (or failure) of partner birds and would thus estimate its poor quality more quickly than when alone. It was found that when in pairs, crossbills did not use the foraging success of their partner bird as information to assess patch quality. The number of cones sampled by the subject bird, and the time spent foraging on the empty tree, did not differ when in pairs from when it was alone. However, when in groups of three, the subject bird spent significantly less time foraging in the empty patch and also searched significantly fewer pinecones before quitting the empty tree, than when alone. This was true for each of the crossbills examined. The results also show that variance in the number of pinecones sampled, and the time spent foraging on the empty tree, was significantly lower for birds in flocks of three, than when either in pairs or when alone. This satisfies another prediction that is made by public information theory (Clark and Mangel, 1984, 1986; Caraco, 1981; Ekman and Hake, 1988; Caraco and Giraldeau, 1991; Ruxton, 1995b; Ruxton et al, 1995), and further supports the use of public information use by crossbills.

The results from this experiment suggest that, similar to the starlings in Templeton and Giraldeau's (1996) study, crossbills are able to use the foraging success of other birds to more accurately assess the quality of a food patch, and modify their patch-quitting behaviour as a result. Both studies demonstrate that the unsuccessful

sampling of group-mates allows some species to assess the quality of patches more quickly than when alone, thus enabling them to quit poor patches earlier. Both also imply that the use of public information may be more important for identifying the quality of poor food patches, rather than rich patches; i.e. enabling foragers to quit those patches containing few prey, rather than specifically assessing the quality of patches containing many prey. Although some crossbills ate more seeds from the 'good' tree in Smith et al's (1999) study, this was not significant. On the other hand, Smith et al (1999) note that the variety between patch quality was limited, and rather extreme – there were only two patch types: 'bad' containing no prey, and 'good' containing a fixed number of prey. The authors suggest that the importance of public information use by crossbills may be underestimated in this study, since it may be more valuable when the difference between quality of profitable patches is more subtle.

The authors examine three possible alternative reasons to explain the results obtained during these trials. Firstly, they mention that when in groups of three, the distribution of prey made available to the two partner birds was different to that available to the birds when in pairs. During paired trials the distribution was the same on both sides of the tree, but when in threes the amount of food given pair of partners was doubled, so that each bird had access to the same amount of food. They suggest that the subject bird may have been basing its patch estimation upon this new distribution. However, the authors think this is unlikely. The trials were run over two experimental periods, in which the order of trial was altered. During the first period the trio trials were carried out after the solitary training, and paired trials. In the second period the trio trials were carried out first, with solitary trials repeated immediately afterwards. The authors suggest that if the subject birds were searching fewer pinecones because they were assuming a different prey distributions after foraging in groups of three, rather than using public information, they would have continued this in the solitary trials immediately following these during the second experimental period. They should have initially searched few pinecones, but gradually searched more as trials progressed over time. This did not happen, and crossbills sampled a similar number of pinecones during solitary trials in both experimental periods.

Smith et al (1999) also argue that the results are not simply due to increased foraging speed because of competition. Firstly, a wire mesh separated the subject and partner birds, eliminating any threat of competition, although this may not necessarily have been recognised by the birds. Birds under the threat of competitors may spend less time sampling cones, as they would want to spend less time at each one, but they should not sample fewer – rather, they should attempt to sample more cones, and hence search more quickly. The is not consistent with the results, since crossbills sampled only half as many cones in groups of three as they did when alone.

The third possibility is that the subject bird simply quit patches when the partner birds did so, simply following their example. This is congruent with public information theory, since it predicts that the mean length of time spent before quitting, and its variance, will decrease (Valone, 1993; Ruxton, 1995b). However, the subject bird was not always necessarily the first to quit the empty tree. Hence, it could not possibly have been following its partner, on all occasions since they were sometimes still in the tree when the subject left. Similarly, at times the subject remained in the tree for several seconds after its partners had quit, also suggesting that the bird was quitting patches based upon its own estimate rather than just copying what the other birds did.

In another study, Coolen et al (2003) demonstrated that nine-spined stickleback were able to distinguish between two feeders offering two different rates of food delivery, by watching the foraging activity of other fish at these sites. The experimental protocol remained the same as that described earlier, the only difference being that both feeders yielded prey - the rich patch offering a higher rate of prey delivery than the poor patch. During the test period 16 out of 20 observer fish visited the rich patch first, and spent significantly longer in the goal zone surrounding the rich patch, than the poor patch. However, these results were not seen in three-spined stickleback, which showed no preference toward the rich patch, suggesting that they could either not differentiate between the two patches, or that they did not use public information in the estimation of patch quality.

The studies of Smith et al (1999), Templeton and Giraldeau (1995a, 1996) and Coolen et al (2003) provide strong empirical evidence that some animals are able use

the foraging success of other individuals to make improved estimates of patch quality, lending good support to public information theory. However, both Smith et al (1999) and Templeton and Giraldeau (1996) also suggest that foragers may only do this when it is easy to acquire such information with any accuracy. In situations where a forager may have to sacrifice it's own foraging time, and thus its own sampling information, public information is ignored.

However, this is not to say that all animals in groups are able to utilise public information for patch estimation, or that they rate it as a high priority in comparison to other aspects of grouping. For example, Vasquez and Kacelnik (2000) showed that starlings (*Sturnus vulgaris)* actually experienced a decrease in their prey capture rates, and remained in food patches longer, when in groups than when alone, which is the reverse of what should be expected. When given a choice they actually preferred to forage in groups, despite the costs incurred to personal foraging. The conclusion was that other benefits to sociality overcame any decrease in immediate foraging efficiency. Livoreil and Giraldeau (1997) also demonstrated that spice finches (*Lonchura punctulata*) foraging in groups consistently depleted food patches to a lesser extent than lone birds, contrary to optimal foraging model predictions. They suggest that this may be because foragers are forfeiting the maximisation of feeding rate in order to remain in the group. Alternatively they suggest that this may be because spice finches are simply unable, or unwilling, to use public information to accurately estimate the decreasing quality of a patch, as was shown in budgerigars, *Melopsittacus undulatus* (Valone and Giraldeau, 1993).

In another recent study, Bergen et al (2004) reported that nine-spined sticklebacks *(Pungitius pungitius*) only exploited the most reliable source of information, when public and personal sampling information conflicted. During the first part of the experiment, fish were placed in experimental tanks which were divided into three sections using transparent partitions. A feeder was placed at each end of the tank, and designated as either 'rich' or 'poor'. Rich feeders offered three bloodworm every 90 seconds, over a 10 minute period. Poor feeders offered three bloodworm after 1 minute 30 seconds, and again after 6 minutes. At times when prey was delivered to the rich patch, but not the poor patch, drops of water in which bloodworm had been

defrosted was dispensed by the poor feeder, to eliminate any difference in olfactory cues between feeders.

Previous to experiments, six groups, each split into two shoals of eight fish, were trained using the feeders for six days. Two groups were trained using the rich feeder 10 times and the poor feeder 8 times, so that private information was 56% reliable. Two groups were trained with the rich feeder 14 times and the poor feeder 4 times, to provide private information with 78% reliability. Finally, two groups were trained for all 18 trials in the rich patch, so that private information was 100% reliable. On the seventh day, each fish acted as a subject, and was placed behind a transparent partition in the central section of the tank. A group of three fish was then placed in each end section, and acted as demonstrators to the subject. Each demonstration lasted for 10 minutes, and were the same as training sessions, except that the profitability of the two feeders were switched, so that each subject observed feeding activity which conflicted with its previous experience. After each demonstration the two groups of fish and the transparent partitions were removed and the subject fish was allowed to swim freely around the entire tank. The location of the fish was recorded every six seconds for 90 seconds, or until it entered the goal zones around one of the two feeders.

As expected, the majority of fish having experienced 100% reliable private information during training sessions visited the rich feeder first. This trend was significant. Those having experienced 78% reliable private information also showed a preference for the rich patch, but this was not significant. Meanwhile, those having experienced 56% reliable information had no preference for either of the two feeders. Following the demonstration phase of the experiment, in which the profitability of feeders was reversed, a significant number of subject fish with 100% accurate private information first visited the patch they remembered as being rich during training (which was now poor), thus disregarding the public information of the demonstrators. They also spent significantly more time in the goal zone surrounding the rich patch according to their training. Fish with 78% and 56% reliable private information showed no preference for either feeder. There was no significant difference in either group over which feeder was visited first, nor the amount of time spent in the goal zone of each feeder. For groups with 78% reliable private information the choice of

feeder visited first was not different from that directly after private training, indicating that these fish were also basing their foraging decisions on private information. However, for groups with 56% reliable information significantly more fish switched the first choice of feeder to that indicated as rich by the demonstrators, thus ignoring personal sampling information in preference for public information.

To examine whether nine-spined were able to remember private sampling information, the authors compared the foraging behaviour in this study with that of a previous study (Coolen et al, 2003). This earlier study was carried out under the same experimental conditions as the one described here, except that the sticklebacks in this study only ever had access to public information – they had no prior experience in this foraging scenario. If they were not able to remember the private sampling information experienced during training, their foraging decisions should not be different from those obtained here, since they would be relying solely on public information. Results showed that significantly fewer fish with 100% and 78% reliable private information based their foraging decisions upon the public information available during demonstrations, thus indicating that they are able to remember personal sampling information. But the foraging decisions of fish with 56% reliable private information did not differ significantly from those with only public information, implying that they are also using only public information to make their foraging decisions.

The results obtained here intimate that fish with (100% and 78%) reliable personal foraging information are unwilling to use the patch sampling information of others as a basis for their foraging decisions. Fish with less accurate personal sampling information (56%), on the other hand, are more likely to use the sampling information of others than their own. The authors suggest that the fish with less reliable personal sampling information (78% and 56%) are more willing to use public information, since they spent equal amounts of time in the goal zones of both feeders, and thus half are using private, and half using public information. There is however one problem with this experimental set-up and consequent interpretation of results. The authors assume that by varying the food returns to fish they are altering the reliability of personal sampling information. Actually the personal sampling information remains perfectly accurate and reliable - it's the food source that is unreliable. Personal

sampling information is simply inferring that a feeder returns food only 78% or 56% of the time, which is true because that is the experimental protocol. In this case the fish are perhaps using public information not to supplement their own personal sampling information, but in an attempt to find a more profitable food source. This misinterpretation should not affect the expected results from this experiment. A fish with unreliable information may indeed prefer to use information supplied by another individual, but so should a fish perceiving another fish feeding at a richer patch. The results could be a consequence of either.

The second part of this experiment examines the extent to which sticklebacks are still willing to use their (totally reliable) private information, when it had not been updated for some length of time. Fish were trained in tanks similar to those in the first part of the experiment, in shoals of ten, over a period of 6 days. On the seventh day each fish was tested for its preference of feeder, as in the first experiment, and those which entered the goal zone for the rich feeder were selected for inclusion in further trials. These fish were then divided into four treatment groups and were given a public demonstration in which the profitability of feeders were switched again, as in the first part of the experiment, each group being shown the public demonstration and tested for preference at different times, depending upon the treatment. One group was shown the demonstration on the first day following private sampling. A second group were tested 3 days after private sampling; a third group after 5 days, and the fourth group after 7 days.

Results show that on the first day after private sampling, a significant majority of fish first visited the feeder which they had learned was rich, according to their personal sample information (which was now poor), thus ignoring the information available to them from public demonstration in favour of their own. Fish in this group also spent significantly more time in the goal zone of the perceived rich patch, than in rich patch indicated by public information. Fish in the groups tested after 3 and 5 days both displayed no preference to first visit either of the feeders. After three days there was still a tendency to spend more time in the goal zone of the perceived rich patch, but this was not significant. After 5 days, there was no difference in the amount of time spent in either goal zone. However, the group tested 7 days after private sampling showed a significant preference for the feeder indicated to be rich by public

demonstration. A significant majority of fish in this group first visited the rich patch according to public information, and spent significantly more time in the goal zone surrounding it, than the patch it had learned to be rich during training. These results suggest that the tendency to rely on reliable private sampling information diminished over time, when conflicting public information is available. Fish are more likely to base foraging decisions upon public information after several days without updating private information.

In a further analysis Bergen et al (2004) use results from Coolen et al (2003), the authors finding that only those fish demonstrated to after 7 days showed no significant difference in feeder preference from the fish in Coolen et al's (2003) study, which had experienced only public information. The similarity in foraging decision between these two groups is good evidence that fish that have not updated their personal sampling for seven days favour recently available public information more strongly. Of the groups examined 1, 3 and 5 days after private sampling, none showed any significant preference for either feeder. This suggests that the fish in this study (Bergen et al, 2004) were not using public information in preference to highly reliable private sampling information, unless the private information was several days old.

The authors conclude from this study that nine-spined sticklebacks are able to weight the value and use of public information differently, depending upon the reliability and age of personal sampling information. When personal information was reliable, and public information conflicted with this, sticklebacks ignored public information. But as reliable personal information aged, and its reliability decayed, they were more likely to use recently acquired public information.

Limited attention

The experiments described here offer ample evidence that some animals at least, are able to use sampling information made available by others, to estimate resource quality, whether it be potential mates, competitors, breeding habitats or food patches, thus sufficiently supporting public information theory. However, it is unlikely that animals are able to acquire an unlimited amount of public information without

restriction, or without incurring some cost. In the context of this thesis, which concentrates on social foraging, such a cost is most likely to be incurred as a loss of personal foraging success, due to limitations in perception and attention. Fernandez-Juricic et al, 2004b) point out that there may not be a distinct trade-off between foraging and vigilance tasks, because the two aren't necessarily mutually exclusive.

Some empirical research agrees with this, although others do not. Studies on anti-predatory vigilance offer a wealth of experimental evidence that animals are constrained in their attention. Lima and Bednekoff (1999) show that dark-eyed juncos (*Junco hyemalis*) lost some ability to detect approaching whilst feeding with their head down. When their head was raised they always detected predators. Thus foragers must terminate feeding whilst looking out for attacking predators. We can perhaps apply this to the sharing of public information. In this experiment the predator was an immature Cooper's hawk, mounted to a pulley which 'flew' the hawk down a chute constructed from transparent plastic sheeting over a wooden frame. Each attack consisted of the hawk being released and 'flying' down along the wire pulley towards the target zone, containing a single junco. The distance from the bird at which it detected the hawk was recorded, and whether it had been feeding (head down) or an unobstructed view of the chute (head up). To avoid the blind-spot directly in front of the birds face, attacks were only made when the bird was lateral to the chute. That this was necessary itself suggests that animals are constrained in their visual attention.

The results from this experiment show that juncos are well able to detect an oncoming attack even when they are engaged in another activity. When the hawk approached against a grey background, and was therefore easily visible, the juncos detected it at an average distance of 10.7 metres. When the hawk was flown against a camouflage background, it was not detected until it was almost three times closer (3.8m). While the birds had an unobstructed view of the chute (head up) they detected the hawk as it emerged from the chute on all but one occasion – a distance of 15 metres. They did this regardless of the hawk's visibility against the background. Although this experiment may not necessarily be realistic in its details, it demonstrates that juncos are impaired in their ability to monitor an aspect of the environment (and an important one at that), when concentrating on a foraging task. Other birds with

similar visual anatomy must presumably suffer the same fate. This is supported by further work on Teal (*Anas crecca*) and shoveler (*Anas clypeata*), by Guilleman et al (2001).

On the other hand, Templeton and Giraldeau (1996) demonstrated that starlings (*Sturnus vulgaris*) would not use sampling information made available by a partner bird if they could not easily observe that partner without interrupting their own foraging activity. Similarly, Smith et al (1999) showed that red crossbills (*Loxia curvirostra*) did not use public information when in groups of two, but they did in groups of three. One explanation for this could be that it was easier for the subject to follow the foraging success of three birds, than that of two birds. Further to this, Bergen et al (2004) suggest that fish will only use public information if their own private sampling information is not totally reliable, or if it has not been updated for some time.

Fernandez-Juridic and Kacelnik (2004) on the other hand demonstrated that although starlings were willing to use the foraging information supplied by foragers in cages next to them, modifying their own feeding behaviour as a result, they were less willing to do so as the space between them and their neighbours increased. The authors suggest that this may be due to the difficulty with which this information could be acquired. But also, as distance increases between individuals, the less likely it is to be relevant to the receiver's own foraging activity. But regardless of this, the study indicates that starlings are able and willing to alter their own foraging behaviour depending upon the quality of the information made available to them by other foragers. Lima and Zollner (1996) found the same thing when examining the effect of spatial separation on vigilance in wild flocks of birds.

In a recent study Franks et al (2003) demonstrated a trade-off in decision making in ants (*Leptothorax albipennis*). They showed that when choosing a new nest site under harsh conditions, they do so more quickly, but as a result tend to choose sites of lower quality. Data from this study shows that these mistakes tend to occur due to poor judgement rather than reduced searching rate. This occurs as a consequence of individual decision making, rather than collective colony decision-making – decreased communication between members of a colony under tough conditions

limits the decision process. This can be likened to limited attention in a cognitively more advanced species.

Several studies in the field of experimental psychology provide evidence that animals are constrained in their ability to concentrate on more than one task. Animals concentrating on one task show a reduced ability to perform another task (Rees et al, 1997; Desimone, 1998). One study carried out by Vreven and Blough,(1998) showed that White Carneaux pigeons (*Columba livia*) were less able to accurately detect target objects not only when the number of non-target objects increased, but also when the number of potential target objects increased. Experimental apparatus consisted of a box with two openings. One opening allowed access to a food tray, and the other to a touch-responsive video screen. The screen showed a 6x6 grid. During trials, each square in the grid displayed one of a list of alphabetical, numerical or punctuation characters. Thirty-five of these were drawn from a list of characters, called distracters: D, G, H, I, K, P, R, T, !, @, #, %, &, *, (,), +, =, [,], {, }, |, /, 1, 2, 3, 4, 5, 6, 7, 8, 9, \, <, >. The remaining empty square displayed a character drawn from another list, called targets: A, E, J, L, N, Q, S, V. The birds had been trained to recognise these target characters during previous experiments, and peck at the grid square containing them.

Each experimental run consisted of a series of 24 individual trials. During each run a bird was shown the display grid containing one target character, and depending upon the trial this target was either displayed alone, or with 11 or 35 distractors. In fixed runs the target character remained constant for all trials, but in mixed runs the target character could be any of the eight characters in the target list. Each run also varied the size of the characters displayed, although the size remained constant throughout each run. A correct response was considered to be when the bird pecked at the column containing the target character rather than at the correct grid square itself, although the authors report that the birds were well able to peck directly at the correct grid square. After a correct response the display screen was cleared, and food was offered with a probability of 0.5. An inter-trial period of 3 seconds then followed before the next trial. An incorrect response was considered to be when the bird pecked at a column not containing the target character, or when no pecks occurred within 7 seconds of the display being shown to the bird. If this happened then the

display was cleared and the inter-trial period began immediately, followed by a repeat of the same trial. If this happened again, the trial was repeated a third time but with no distracters. This continued until the pigeon elicited a correct response. This data was not included in the final analysis. The birds found it more difficult to find the target character when the screen display size was smaller. But results also show that the pigeons were less able to accurately identify the target character when there were more distracters in the grid too. Similarly, their accuracy was lower during mixed trials, than for fixed trials. Both of these latter results strongly indicate that pigeons are limited in their attentional abilities, since they were less able to perform a task when the environment contained more elements to attend to.

Another study by Dukas and Kamil (2000) reported that blue jays (*Cyanocitta cristata*) were able to increase their performance at a foraging task in the centre of the visual field when it was made more demanding, but their ability perform a secondary (peripheral) task suffered as a result. Blue jays were positioned on a perch in front of a computer screen, displaying three target areas - one central circle and two peripheral elipses. Birds were trained to identify shapes on the screen, representing two different types of prey: caterpillar targets appearing in the central circle, and moth targets appearing in the peripheral elipses. During the first part of the experiment the target caterpillar appeared in the central circle, hidden among a number of non-target items. The number of non-targets varied from trial to trial. The target caterpillar only appeared in 50% of trials; birds were rewarded with food when they correctly detected the presence of the target caterpillar and pecked at the screen, and punished for pecking when no target was shown. It was found that the time taken to detect whether the target caterpillar was present or not was higher when the number of non-targets was also higher. The difficulty of the central foraging task could be altered by varying the number of non-target items.

The second part of the experiment followed the same protocol as the first part, with target caterpillars being shown in 50% of trials in the central circle, the difference being that a target moth was shown in either of the peripheral elipses in 25% of trials. The subject birds task was to correctly detect which of the three target areas contained the target prey item and peck at the corresponding part of the screen. In all trials the target areas contained a number of non-target items. The number of non-targets

remained constant between trials in the peripheral elipses, but once again the number of non-targets varied in the central circle. Birds were rewarded with a food item when pecking the correct target area, and punished with a 1 minute delay for pecking the wrong target area, and a 5 second delay if no peck was made at all. The length of time taken to make a decision and peck at one of the three target areas was not significantly different, regardless of the number of background items in the central target area. The subject birds were spending the same amount of time in detecting whether the prey was in the central of peripheral target areas, whether the central foraging task was easy or difficult. However, when the number of non-target items in the central circle was higher, and thus more demanding, the birds made significantly more incorrect pecks - they were more likely to mistake the location of the target prey item. These results suggest that, although blue jays can increase their performance at a task by directing more resources to that task, there are limits to the amount of resources that can actually be directed, and so other, secondary tasks will suffer. Dukas and Kamil (2001) found similar results supporting this, when blue jays had to divide their attention between two different types of prey. In terms of foraging and public information use, both of these studies imply that a forager may be well able to monitor other members of a feeding group to exploit their patch sampling information and feeding success, but this may well reduce their own personal foraging success.

Conclusion

This examination of the empirical literature shows that in certain situations animals in groups can and do use social information supplied by others, and are able to benefit from this in terms of their foraging success. However, despite the work showing that animals are limited in their attentional abilities, little has been done to examine the effects of limited attention on foraging activity. Furthermore, even less consideration has been paid to the effects that attentional limitations may have on the use of social and specifically public information, in group foraging animals. Hopefully the work presented in thesis will provide general framework models that can be used to make testable predictions for future empirical studies.

CHAPTER 3

PUBLIC INFORMATION AND PATCH ESTIMATION FOR GROUP FORAGERS: A RE-EVALUATION OF PATCH QUITTING STRATEGIES IN A PATCHY ENVIRONMENT

ABSTRACT

Classical foraging theory states that animals feeding in a patchy environment can maximise their long-term prey capture rates by quitting food patches when they have depleted prey to a certain threshold level. Theory suggests that social foragers may be better able to do this if all individuals in a group have access to the prey capture information of all other group members. This will allow all foragers to make a more accurate estimation of the patch quality over time and hence enable them to quit patches closer to the optimal prey threshold level. We develop a model to examine the foraging efficiency of three strategies that could be used by a cohesive foraging group to initiate quitting a patch, where foragers do not use such information, and compare these with a fourth strategy in which foragers use public information of all prey capture events made by the group. We carried out simulations in six different prey environments, in which we varied the mean number of prey per patch and the variance of prey number between patches. Groups sharing public information were consistently able to quit patches close to the optimal prey threshold level, and obtained constant prey capture rates, in groups of all sizes. In contrast all groups not sharing public information quit patches progressively earlier than the optimal prey threshold value, and experienced decreasing prey capture rates, as group size increased. This is more apparent as the variance in prey number between patches increases. Thus in a patchy environment, where uncertainty is high, although public information use does not increase the foraging efficiency of groups over that of a lone forager, it certainly offers benefits over groups which do not, and particularly where group size is large.

INTRODUCTION

Optimal foraging theory, mostly centred on Charnov's marginal value theorem (Charnov 1976), predicts how long an individual forager should remain feeding in isolated and depleting food patches, before quitting to move to the next patch, with the aim of maximising long term capture rates and thus fitness. Much work has been carried out in this field, and several models have been developed to explain foraging behaviour based upon this theorem. However, many animal species are known to live and feed in groups (Krause and Ruxton 2002) and although there are many theories which suggest benefits to aggregation (Krause and Ruxton 2002) few offer any direct benefits in terms of foraging. One theory which does so, suggests that animals feeding in groups may prevent a reduction in their prey capture rates by utilising prey capture information supplied by other group members (Clark and Mangel 1984, 1986, Valone 1989, 1993). This is generally termed public information use. Foraging groups deplete prey resources at a rate faster than for a lone forager. However, this means that information about the quality of a patch is also being obtained faster by the group. If all individuals are able to recognise when each other forager makes a prey capture, they should be able to make an accurate estimate of this decreasing patch quality, allowing them to quit patches close to the optimal threshold level.

Valone (1993) examined the effect of public information use in cohesive, socially foraging groups, in a environment in which food is distributed unevenly between a series of discrete patches. In such an environment, the distribution of prey between patches may be known to a forager, but since the number of prey in each patch may be quite variable, the exact number of prey in any patch is unknown. Foragers must therefore estimate the quality of each patch through sampling as they search for food, in order to decide when they should quit the patch and move to another. Iwasa et al (1981) developed a formula which generates a good estimate of patch quality in such an environment for a lone forager, where only the distribution of prey between patches, the number of prey items caught in a patch, and the time spent searching in a patch, are known to the forager. Valone (1993) presented a group foraging model based on Iwasa et al's (1981) estimator equation. Groups remained tightly cohesive at

all times, with all individuals forced to enter and leave patches simultaneously. However, within a patch foragers search randomly and independently of each other and often maintained different estimates of patch quality, according to their own individual prey capture success. Thus some conflict must occur between individuals in a group as to when they should leave a patch. Valone examined three different patch quitting strategies to dictate how such groups decide when to leave a patch. He compared the foraging efficiency of these with that of groups using public information of all prey capture events made by the group. Since all foragers acquire the same patch information in these groups, they will all share the same estimate of patch quality and so will want to leave the patch at the same time.

Valone showed that sharing public information does indeed benefit group foragers, in comparison to those groups which do not. Groups using public information were able to quit patches closer to the threshold quitting value, and experienced higher capture rates, than those using the other three patch quitting strategies, although they were never as successful as lone foragers. However, we believe that Valone's implementation of Iwasa et al's (1981) estimator is not entirely correct, causing inconsistencies in his model and thus making proper evaluation of his results more difficult. Here, we present an revised version of Valone's model and re-evaluate the assumptions made by public information theory.

MODEL DESCRIPTION

The marginal value theorem (Charnov 1976) states that foragers should remain in a food patch until their instantaneous capture rate has fallen to the average capture rate they would expect to obtain over the environment as a whole - this is the marginal capture rate and should be equalised over all patches visited (Charnov 1976, Brown 1988). In groups, foragers using public information of all prey capture events should be better able to do this, since each forager will have more information of the patch quality at any time, so enabling them to generate a more accurate estimate of the true patch quality, and thus allowing them to quit patches closer to the marginal capture rate.

A deterministic model such as Charnov's (1976) is limited here in two ways, because it assumes that food is obtained by foragers continuously and that a forager automatically knows, at any point in time, the exact rate at which food is being found (Oaten 1977). Unfortunately, prey is rarely acquired at a continuous level by a forager, but is more often found stochastically, in discrete packages (i.e. a food item - a bird, a seed, or berry). So more realistically, a forager will need to know how many prey items it should leave in the patch when it quits, rather than a specific rate of capture. Foragers should therefore try to quit a patch when they have depleted it to a threshold number of remaining prey items - we call this the optimal value of C - which should be equalised over all patches visited, as would the marginal capture rate. This is the LOC, or left-over constant described by Green (1988). But in order to do this, foragers must know how many prey items remain in a patch at any time (Green 1988). Again, this seems an unrealistic assumption to make for most natural ecological situations. It seems far more likely that foragers will only have some idea or expectation of how prey is distributed throughout the environment, rather than absolute knowledge of the quality of food patches, and they will form an estimate based upon this prior expectation and their experience foraging in a patch. In this case the model suggested by Charnov (1976) does not always hold true (Green 1980, 1988, Olsson and Holmgren 1998). When there is uncertainty about patch quality it may be more valuable for a forager to spend a longer time searching in order to obtain more information about its true quality. However, providing a forager has prior knowledge of how the prey is distributed in its environment (i.e. it feeds there frequently, so has an expectation of the distribution of prey likely to be found in a patch), and compares its continued foraging success against this expectation, it can still produce a pretty good estimate of the true quality of a patch and hence when to leave it (Iwasa et al 1981).

Prey distribution

Valone (1993) models a scenario where prey items are distributed between patches according to a negative binomial distribution in an attempt to mimic a patchy environment, with distribution parameters λ and α. A property of the negative binomial distribution is that the variance is higher than its mean, so that the actual number of prey in each patch may be highly variable and while many patches contain

very few (or zero) prey items, a few patches will contain many prey. Valone defines the distribution parameters as $\lambda = 500$, and $\alpha = 0.3$, so the number of prey items in any patch before the foragers arrive on it (X) has a negative binomial distribution with a mean $\lambda\alpha = 150$ and variance $\lambda\alpha(1+\alpha) = 195$. However, attempting to use patch sampling to discriminate between patches is effective "if and only if the between-patch variance of prey abundance is sufficiently large" (Iwasa et al, 1981), and so here we expand on Valone's (1993) work by simulating several prey environments, to examine the effects of public information use under different levels of patch variation. Figure 3.1 shows an example plot of a negative binomial distribution, for parameter values $\lambda = 6$, $\alpha = 25$, in comparison to one using Valone's (1993) parameter values.

In our model the number of prey in each patch is found using the random number rejection technique (Evans et al 1993a), where α defines the probability of finding prey, and λ defines the number of attempts in which prey is not found until the x^{th} success. We simulate foraging activity in six different prey environments, where we vary both the mean number of prey per patch, and the variance of prey between patches. We model two main prey environments, with a mean number of prey items per patch = 150 (small) and 250 (large). For each of these environments we model patches with three types of variance: small, medium and large (mean = 150: variance = 1650, 2400, 3900; mean = 250: variance = 2750, 5250, 8062.5).

Inter-patch travel time

Since foragers can only feed within patches, they must travel between patches in order to feed, and thus incur a travel-time cost as they do so. This ultimately affects the length of stay in each patch. We assume inter-patch travel time (T) to be a function of the size of the group (N), so that as group size increases the time spent travelling between patches decreases proportionally:

$$T(N) = \left(\frac{T_1}{N}\right) \qquad (1)$$

where T_1 = the inter-patch travel time for a lone individual. We follow Valone (1993) and Ruxton (1995b) and assume a value of $T_1 = 400$. A single forager thus takes 400

time units to travel between patches. Using this function, a group of two individuals takes half this time to find a new patch, so T = 200. A group of 3 individuals incurs only a third of this T_1, so T = 133. This is an ideal situation, and is probably unlikely to be true in nature. In a wild situation animals are likely to become less efficient at searching an area as group size increases, because the chance of two or more animals searching in the same place at one time increases, and search-overlap occurs (Ruxton 1995a, Ruxton and Glasbey 1995). However, this function between group size and search rate is a simple one to model, and is a suitable and convenient simplification for the simulations we are running here.

Searching for food

We assume that foragers have knowledge of the prey environment they are feeding in and have a prior expectation of the mean number of prey items ($\lambda\alpha$) when they enter a patch, and the variance between patches, but do not know the actual number of prey items existing on any one patch (X). Prey are hidden so foragers do not know whether they will find prey on each search attempt or not. Each food item has equal energetic value and can only be found whole, so a forager either finds and consumes a prey item or doesn't, and so scores either 1 or 0, respectively. Prey is not replaced once found and since foragers search randomly and independently of other foragers, prey decreases as it is exploited and the probability of finding a prey item decreases linearly with the number previously found.

Each forager searches a patch at a rate S_1; i.e. they make S_1 search attempts per unit time. Since patches initially contain X prey items, the probability of finding prey on each search attempt is X/patchsize. Like Valone (1993), for convenience and simplicity we assume here that patches contain a maximum of 500 prey items. Although by definition patches described by a negative binomial distribution do not have a theoretical upper limit to their size, we cannot accurately calculate searching rates without ascribing such limits. Using the values of λ and α we have chosen, we can be confident that fewer that 1% of patches will contain more prey than this arbitrary limit. In trial simulations, replacing this value of 500 with 5000 did not lead to any differences in our results, but dramatically slowed simulation time.

All foragers in a group search the patch at the same rate, and thus a group of N foragers find prey items at a rate R(X), which is given by:

$$R(X) = \frac{XNS_1}{500} \qquad (2)$$

Since finding prey is a Poisson process, the time taken to find a prey item can be found stochastically using the exponential distribution with a mean 1/R(X). All foragers are assumed to be equal in foraging ability, and so each prey item is found and is allocated to a random forager. Prey resources then decrease by one and the time taken to find the next prey item thus becomes: (1/R(X-1)). This departs from the models of Valone (1993) and Ruxton (1995b) because it effectively means that time is continuous in our model, rather than being counted in arbitrary time steps.

Patch estimation and patch quitting strategies

Iwasa et al (1981) suggests that for a lone forager feeding in a patchy environment the best estimate (E) it can make of the remaining number of prey is a function of the time spent foraging on the patch (t), and the number of prey items taken in that time (n), and is described by the estimator equation:

$$E\ (n,t) = \frac{\lambda + n}{e^{At}\left(\frac{\alpha+1}{\alpha}\right) - 1} \qquad (3)$$

where A = the searching rate (the fraction of the patch searched per unit time).

With public information use

In a situation where all foragers have access to public information of all prey capture events, each will have exactly the same knowledge as each other individual in the group. We can re-phrase the above estimator function to incorporate our definition of group patch searching rate:

$$A = \frac{NS_1}{500} \qquad (4)$$

(where the N = the number of foragers in the group, S_1 = the search rate of one individual, and 500 = the assumed size of the patch). Equation (3) thus becomes

$$E_N(n,t) = \frac{\lambda+n}{\exp\left(\frac{NS_1t}{500}\right)\left(\frac{\alpha+1}{\alpha}\right)-1}. \quad (5)$$

We call this strategy the Totalinfo strategy.

Without public information use

In groups which do not have access to public information each individual does not know the true value of n. A specific individual, i, knows only how many prey items it has found itself (n_i), and so must use its own foraging success to produce an estimate of patch quality. It can do this by multiplying this number, n_i, by the number of individuals in the group, and so the estimator function in equation (3) becomes:

$$E_{i,N}(n,t) = \frac{\lambda + Nn_i}{\exp\left(\frac{NS_1t}{500}\right)\left(\frac{\alpha+1}{\alpha}\right)-1} \quad (6)$$

But since foraging is an inherently stochastic process, each individual's estimate is likely to be different from that of other individuals in the group, and there will be some disagreement over when to quit a patch. In order to maintain group cohesiveness, the group must employ rules to govern exactly when to leave the patch. We use two of the patch quitting strategies suggested by Valone (1993) which may be used by non information sharing groups to achieve this:

1) First - the group leave with the first individual whose estimate, E, falls below the threshold prey value, C.

2) Leader - the group leave when the E of one particular individual, for example the most dominant member of the group, falls below the prey threshold, C.

We also use a third strategy suggested in a similar study by Ruxton (1995b):

3) Paired - the group leave when the estimate, E, of any two individuals falls below the prey threshold, C.

However, despite the convincing results obtained by Valone (1993), we believe that this model contains an inconsistency in the use of Iwasa et al's (1981) estimator function. Within patches, each forager estimates the number of prey items that remain using this estimator, but the method Valone (1993) uses to calculate the rate at which foragers find prey (R(X)) conflicts with an important assumption of this function. The estimator remains true only if prey resources in a patch decrease in

proportion with the number taken by foragers: $R(X) = NS_1(X/P)$, where N = the number of individuals in a group, S_1 = the search rate of one individual, X = the number of prey remaining in a patch and P = the size of the patch (the maximum number of prey a patch can contain). Valone (1993) breaks this assumption by describing the rate at which foragers find prey, R(X), with a sigmoid curve (see his Figure 1). This implies that the probability of finding the next prey item does not decrease linearly with the number of prey already found (n), and thus the estimator equation cannot be used correctly as the two statements contradict with each other. No explanation is given in his paper as to how he obtained this function.

The aim of this paper is to re-examine the foraging efficiency of groups using the above three non information sharing strategies (First, Leader and Paired) in comparison with groups which use public information of prey capture events occurring in a patch (Totalinfo). We expand on the work of Valone's (1993), and Ruxton (1995b), by increasing the range of prey environments examined. We also consider a larger range group sizes.

Optimal values of C

Here, we assume that foragers have evolved to use the optimal value of C in the environment in which it feeds. Since this value is dependent upon the average travel time between patches, it also seems likely that this value will vary depending upon the size of the group, and the efficiency with which foragers utilise their search time in a patch. Other models, (e.g. Valone 1993, Ruxton 1995b) adopt patch quitting thresholds which seem arbitrary and may not necessarily be optimal. We simulate foraging behaviour over a series of patches, forcing foragers to quit a patch when they estimate patch quality to have fallen to each possible value of C, using each of the patch quitting strategies described above (First, Leader, Paired and Totalinfo) to estimate C. This is repeated for a range of group sizes (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 20, 50, 100, 500, 1000), in each of the six prey environments described above. Mean prey capture rates were recorded for foragers quitting patches at each of these C values. In this way we find the optimal quitting value of C particular for each combination of group size and quitting strategy.

Each simulation was repeated 500 times and the mean capture rate for groups quitting at each value of C was calculated in each trial. When plotted, the resulting curves shows the success of foragers leaving patches at each quitting value of C. The optimal value C was the value which produced the highest capture rate in each simulation (i.e. the peak of the curve). Figure 3.2 shows the optimal values of C obtained for each of the six prey environment simulations.

RESULTS - OPTIMAL C VALUES

Finding the optimal value of C - with public information use

In all simulations the optimal value of C for groups using public information remained constant over all group sizes (Figures 3.2 - only results for patch mean = 250 are shown). As group size increases there is no effect on the optimal point at which foragers should quit a patch. Groups sharing public information effectively act as one super-individual: they deplete a patch (on average) at a rate directly proportional to the size of the group, but since inter-patch travel time is inversely proportional to the size of the group these two factors cancel each other out. Considering this, we should not expect the optimal value of C to change with increasing group size.

In patches with a prey mean of 250 the optimal value of C is higher than those with a prey mean of 150. In patches containing a mean of 150 prey items foragers should quit when approximately 50 prey remain (results not shown), while in patches containing a mean number of 250 prey, they should quit patches when approximately 90 prey remain. This finding agrees with classical optimal foraging theory since foragers should harvest fewer prey from patches when feeding in a richer environment.

In the same way, foragers should harvest patches to a lower level when the travel time between patches is longer, since increasing inter-patch travel time decreases the richness of the environment by decreasing prey density. Similarly, larger groups should have to harvest patches to a lower level, because this has the same effect on each individual as decreasing prey density, although indirectly. However, in these

simulations we are not merely increasing the size of the group but also simultaneously decreasing the value of travel time per individual. So, although a group of N individuals receive only 1/Nth of the available prey resources, they also only incur 1/Nth of the travel cost. As explained above, the two cancel each other out and so we should not expect to see any change in optimal C values with changing group size, since the relative prey density remains constant.

Finding the optimal value of C - without public information use

In all three non information sharing strategies (First, Leader, Paired) the optimal value of C decreases with increasing group size (Figure 3.2 - only results for patch mean = 250 are shown). Thus, in order to behave optimally, larger groups using these strategies must harvest all patches to a lower level of prey before quitting. This is important because it immediately suggests that groups using these strategies are not as efficient as groups which share public information, and are incurring some cost as a result. Classical foraging theory states that foragers should deplete patches to a lower level when the travel cost between patches is higher, but since travel time does not differ here between strategies, this cost must be originating elsewhere. The only difference between each group in these simulations is the strategy employed to quit patches, and so this cost is likely to arise because of the constraints placed on groups by the particular patch quitting strategy being used.

These simulations calculate the optimal value of C at which foragers should quit patches when using each of the patch quitting strategies described (First, Leader and Paired). Foragers estimate patch quality and since no information is shared each individuals estimate will vary according to their own foraging success. Each will have a different approximation of the patch quality and this will create conflict within the group. Each of these strategies aims to resolve this by relying on the estimate of one particular individual. But as a result of this the time at which the group quit the patch will be biased towards that individuals foraging success and not necessarily represent the groups overall success.

For example, in the First strategy the group will leave patches with the first individual that estimates the patch to be below the threshold level. Since the first individual will by definition be the one experiencing the worst foraging success, it seems likely that

the group will probably leave most patches too early, thus not using them to their full potential. This inaccuracy in patch estimation and quitting is a cost to the group. Groups using this strategy must therefore harvest each patch to a lower level in order to make up this cost, just as they should if travelling further between patches. So, the extent to which a forager acts optimally in non public information sharing groups will depend upon the constraints placed upon them by the patch quitting strategy employed by the group. The optimal value of C for each group will thus depend upon the quitting strategy employed.

This explanation is demonstrated further in Figure 3.3. We ran an extra simulation using the First strategy, but made them quit patches at the optimal C values obtained for the Totalinfo strategy, which are higher and remain constant. We assume that these optimal C values are perfectly optimal, i.e. the 'best' values that could possibly be used for a given prey distribution (it is intuitive that the values obtained by Totalinfo groups would be the best possible, because of the nature of the strategy). Figure 3.3 shows that when the groups using the First strategy aim to quit patches at the 'perfect' optimal value of C, they actually do far worse than if they use the optimal C values obtained for the First strategy. This value of C is optimal only for groups sharing information. It is sub-optimal for groups using the First strategy. Forcing them to quit patches at this value does not allow them to make up the cost incurred as a consequence of being inefficient. The cost that non public information sharing groups incur because of the constraints placed on them by the patch quitting strategy cannot possibly be made up if they try to behave 'perfectly'. The best they can do is try to make up the cost as best they can, i.e. by adjusting their threshold value of C and depleting patches to a lower level before quitting.

Ruxton (1995b) suggested that groups quitting patches when two individuals want to leave (Paired strategy) will fare better than those using the First strategy because the likelihood of quitting due to random bad luck will be reduced - two individuals must both be experiencing bad luck at the same time. The patch is more likely to genuinely be poor. Optimal values of C were also consistently higher for groups using the Paired strategy (Figure 3.2) than those using the First strategy, in all expect the highest group sizes, thus supporting Ruxton's (1995b) hypothesis. In groups containing 100, 500, 1000 individuals, as for the First strategy, the optimal value of C

was close to zero, indicating that the foragers should try to remain until the patch is almost exhausted of prey before quitting. Thus in both the First and Paired strategies, foraging in large groups is very inefficient, incurring a heavy cost and therefore requiring that they harvest each patch to a lower prey level before quitting.
Results for the Leader strategy show that optimal C values are higher than those of both First and Paired strategies, for all group sizes. Hence, groups using the Leader strategy are more efficient foragers than both First and Paired groups, and suffer a lower cost as a result. The Leader strategy relies on the estimate of one specific individual to decide when to quit patches, and thus these groups will not always leave patches too early. Sometimes the leader individual will be the first to want to leave a patch, but it will also sometimes be the last, and all other ranks in between. On average then, the leader individual will neither want to quit patches too early, nor too late, but when it is best to do so.

Foraging efficiency - patch quitting in cohesive groups

We used the optimal values of C obtained in the above simulations as threshold prey patch quitting values to assess the foraging efficiency of the four strategies described above. We simulated foraging activity, in which groups using each of the above strategies visited a series of 500 patches per simulation with the aim of quitting at the corresponding optimal C value, in order to maximise foraging efficiency. Each simulation was repeated 2000 times. It has been shown previously (Green 1988, Olsson and Holmgren 1998) that for a negative binomial prey distribution a forager should not strictly quit patches when its estimate of patch quality has fallen to a constant threshold level, in order to maximise its long term prey capture rate. During early stages in a patch the forager should ignore low patch estimates, since there is a chance that this estimate will increase again after further searching. However, we do not expect that our simplification of using a constant patch quitting threshold of prey (optimal C) will qualitatively effect our results, and this simplification greatly reduces our already considerable computational requirements.

Patch estimation and quitting strategies

There are several ways in which foraging efficiency can be analysed. Prey capture rate is perhaps the most important here, since this is a direct measure of the amount of food eaten by a forager in a given time. Foragers with the highest capture rate are

thus maximising the amount of food they consume. We calculate the total number of prey items which have been consumed by the group, divided by the total time spent foraging (including inter-patch travel time), and divide this by the number of individuals in the group, for each simulation. This gives us the feeding rate of each individual forager.

In order to maximise prey capture rates, foragers should try to quit patches when they have depleted the number of prey items remaining to the optimal value of C. We assess the ability of foragers to do this by subtracting optimal value of C from the value of C at which they actually quit a patch. The closer this difference is to 0, the better the foragers are able to quit patches at the optimal value of C. We calculate the mean difference between actual and optimal C over all patches in each simulation. However, considering this mean value on its own can be misleading, since foragers may be over- and under-utilising the patch by a great many number of prey items, while the mean would still indicate that they're quitting patches close to the optimal value of C. To counter this, we also look at the coefficient of variation of the quitting values of C over all patches visited in each simulation. This gives us the level of variation between the quitting values of C obtained by each group. A low coefficient of variation suggests that the group is consistently quitting patches close to a given value. Using both of these tools in combination offers a good measure of the ability of a group to quit patches at a value close to the optimal C, and how consistently they do this.

RESULTS - PATCH ESTIMATION

With public information use

Prey capture rates - In all simulations the capture rates of groups sharing public information remains constant for group of all sizes (Figure 3.4 - only results for patch mean = 250 are shown). Increasing the variance in prey number between patches does not affect capture rates by group foragers sharing public information. However, by altering the average patch quality mean capture rates do change. Where the mean prey number is 250 the prey capture rates are approximately 0.2, while for a mean of 150 the capture rates are 0.12, so decreasing as the patch mean decreases.

Quitting patches at optimal C - In all simulations the difference between the actual quitting value of C and the optimal value of C remains close to 0 for Totalinfo groups of all sizes (Figure 3.5). Similarly, the coefficient of variation remained constant for all group sizes, in each simulation (Figure 3.6). Thus, group foragers sharing public information are able to quit patches not only almost perfectly close to the optimal value of C, but they to do so consistently, despite any increase in the prey variance between patches and regardless of group size.

Without public information use

Prey capture rates - In both of the prey environments used here (patch mean = 150, 250) where the variance in prey number is low (variance = 1650, 2750 respectively), groups using the First strategy obtain capture rates similar to lone foragers, but this decreases slightly with increasing group sizes (Figure 3.4). As variance between patches increases, however, capture rates decrease more markedly with increasing group size, suggesting that larger groups suffer lower foraging efficiency in comparison to smaller groups, and also groups sharing public information. Interestingly, the lowest capture rates are not seen by the largest groups in any of these simulations. In groups of 100 individuals and over, these suddenly increase again. This is likely to be because in extremely large groups the number of prey taken in a given time increases in comparison to smaller groups, so the number of prey remaining is closer to the optimal value of C when groups leave. In this model an individual makes its estimate of patch quality by multiplying its own foraging success by the number of individuals in a group. As group size increases this becomes a more and more unrealistic assumption, but it is actually beneficial when the patch is being harvested so quickly because it acts as a kind of early warning system in large groups. Looking at the First strategy, in small groups this method of estimation often means that the groups quit patches too early. But in larger groups the patch becomes depleted much more quickly and the number of remaining prey is genuinely lower, so these groups no longer quit so early.

This trend is repeated almost exactly in groups using the Paired strategy. In smaller groups there is some evidence supporting Ruxton's (1995b) theory that relying on the estimate of two individuals, will reduce the likelihood of quitting patches due to the bad luck of one individual, as the Paired strategy shows slightly higher prey capture

rates than the First strategy (Figure 3.4). But in larger groups again this advantage is lost because it prevents foragers quitting patches, when in fact it would be beneficial to do so.

For groups using the Leader strategy, capture rates are not independent of group size, as theorised by Ruxton (1995b) but decline at a similar rate to those of First and Paired strategy. But in contrast to these two, this decline continues as group size increases. Because the Leader strategy relies on the estimate of one specific individual to initiate quitting a patch, rather than just any individual, there will be a tendency to remain feeding in patches which are poor if the leader is still successful, but also to quit patches too early if the leader is not so successful. In large groups, even a small amount of time can mean a big difference in the number of prey actually found in each patch, so the number found between patches will be very variable, thus having a profound effect on capture rates.

Quitting patches at optimal C - For lone foragers, the difference between the quitting and optimal value of C was 0, or close to it, in all simulations (Figure 3.5). For the First strategy, as group size increases this difference also increases, so foragers are leaving patches increasingly earlier in larger groups. This supports the hypothesis that foragers using this strategy may be vulnerable to 'runs of bad luck' (Valone 1993, Ruxton 1995b). This loss becomes quite substantial, since groups quit patches as many as 100 prey items too early. However, in the largest groups, this difference decreases again, supporting the explanation above, that larger groups deplete patches more quickly and so when First groups quit patches it is genuinely becoming poor - the number of remaining prey being closer and closer to the optimal value of C on quitting as group size increases.

The coefficient of variation in quitting C also increases with increasing group size, indicating that First groups quit patches less consistently at a given value of C as group size increases (Figure 3.6). Large groups sample more of a patch than small groups, so there is a potential for greater variance in the estimates between individuals over time. Since the First strategy draws from only one extreme of this sample (i.e. the lowest) there is a greater chance of this deviating from the average. However, in the largest groups the variation in the number of prey on departing a

patch decreases again and levels off at a constant value. In very large groups, foragers will tend to quit patches immediately, because a forager finding prey assumes that each other forager has also done so, and the patch must therefore be empty. For example, in a group of 500 individuals, a forager finding prey will immediately assume that all other 499 members of the group have also found prey. Since the patch is expected to only contain a mean of 250 prey items the forager therefore assumes it is empty and will want to quit straight away. In such a short time spent in each patch the variability in the number of prey taken by the group will be smaller and so the actual quitting value of C remains relatively constant between patches.

A similar pattern to this is seen in groups using the Paired strategy, with the difference between quitting C and optimal C, and the coefficient of variation in quitting C, both increasing with increasing group size, and then dropping and levelling off in the largest groups (Figures 3.5 and 3.6). However, for the Paired strategy the difference between quitting C and optimal C is smaller than for the First strategy - these groups quit patches closer to the optimal value of C than groups using the First strategy. This supports Ruxton's (1995b) theory, that groups relying on the agreement of two individuals to quit a patch will be less susceptible to the bad luck of one individual. However, the coefficient of variation in the quitting value of C is higher for this strategy (Figure 3.6). This is likely to be because the group remain in the patch for a longer time, thus allowing greater variation to build up in the number of prey taken between patches.

Where group size is small, the Leader strategy was able to quit patches at a C value close to the optimal, similar to groups using public information (Figure 3.5). But as group size increases above 10 individuals, Leader groups quit patches progressively earlier. In all but the largest groups, the Leader strategy quits patches closer to optimal C than First or Paired groups, but when group size is very large this benefit is lost because of the improvement in patch quitting ability seen by the First and Paired strategies.

The coefficient of variation in quitting C for the Leader strategy increases with group size, and falls again at the higher group sizes (Figure 3.6). When group size is fairly

small, this variation is similar to that of the First group. However, when groups contain more than 10 individuals, this continues to rise and so this becomes worst of all the strategies. Again this can be explained by the rate at which a patch is depleted in larger groups. Both the Paired and the Leader strategy reduce the vulnerability of foraging groups to quitting patches because of the bad luck of one individual. This relies on the assumption that patches are good in quality (i.e. they contain a number of prey higher than the optimal C). As group size increases prey are depleted considerably more quickly than in small groups, and the patch is much more likely to actually be poor. It should be no surprise then that the best strategy at avoiding premature patch-quitting when group size is low, is actually the most detrimental when group size is large, *because* it inhibits patch-quitting.

DISCUSSION

The results presented here show fairly conclusively that sharing public information does give an advantage, in terms of foraging efficiency, to animals feeding in cohesive groups in an uncertain environment. In groups which do not share public information each forager samples only a fraction of the patch, and its estimate of patch quality is totally dependent upon its own foraging success. By assuming that each other forager experiences the same foraging success as itself, the variability in patch estimate between individuals may be very high, particularly in large groups. It follows that each forager is quite likely to have a very different estimate of patch quality and so will want to leave the patch at a different time to other individuals in the group (Valone 1993). Where groups are tightly cohesive this is impossible and certain rules must be employed to determine when the group can actually quit the patch. Thus foragers may suffer because they cannot necessarily quit patches when they want to, and will be forced to quit when they do not want to. Groups using public information overcome this, because every individual knows exactly how many prey have been found in a patch at any one time. Since all foragers share this estimate of patch quality they therefore agree over when to quit a patch (Clark and Mangel 1984, 1986, Valone 1993).

These simulations show that sharing public information enables groups to quit patches close to the optimal prey threshold level, regardless of group size. This supports the conclusions of Valone (1993) and Ruxton (1995b), despite the differences between these models and the one presented here. This is emphasised in environments which are highly variable, in which the quality of each food patch is unpredictable (Clark and Mangel 1984, 1986). Valone (1993) suggested that groups sharing public information will be better able to estimate patch quality and thus quit them closer to the optimal C. He notes that groups not sharing public information will be impeded in patch quitting by their conflicting patch estimates, and patch quitting will become less accurate as group size increases. In fact Valone takes this further by proposing that groups sharing public information will experience an increase in capture rates, as groups get larger.

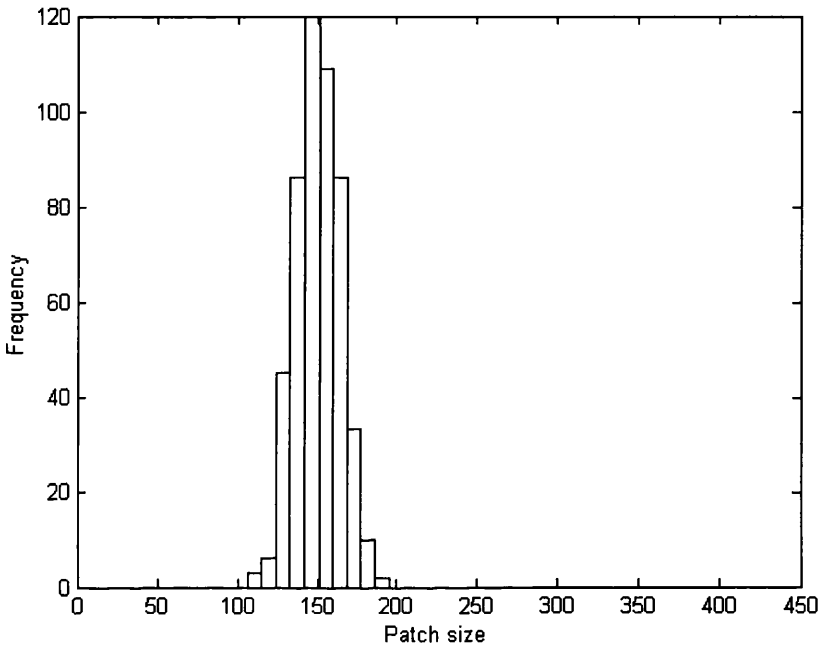
Our results also show that public information use does not offer benefits to groups over lone foragers. Each individual in a group may generate a more accurate estimate of patch quality because it is acquiring information from a greater number of sources, but this does not enable them to quit patches closer to the optimal value of C, nor does it offer higher capture rates. This is also in agreement with previous work (Clark and Mangel 1984, 1986, Valone 1993).

The benefit of public information use is highlighted here by the examination of optimal C values between strategies. Previous studies have adopted arbitrary patch quitting values (Valone 1993, Ruxton 1995b), which may not necessarily be optimal, and in fact may be detrimental to foragers. We show that the point at which foragers quit patches is heavily dependent upon their efficiency as foragers and also as patch quitters. Foragers which are not efficient, for example because they are poor at searching for or handling prey, or because, like here, they are restricted in their freedom to quit patches, will suffer some cost which ultimately affects the extent to which they must harvest a patch in order to maximise feeding rates - this is akin to increasing travel time between patches. It is particularly interesting to note that even when using the optimal values of C obtained for each non public information sharing strategy, these groups suffer in comparison to those using public information. This emphasises further the advantage groups can gain by using public information.

In summary, although sharing public information does not offer an advantage to groups over lone foragers, it does offer several benefits over foragers in cohesive groups. Such groups face restrictions in their freedom of movement and use foraging time less efficiently. Sharing public information prevents this by ensuring that each forager has the same estimate of patch quality, thus removing any conflict over when the group should quit each patch. The work presented here suggests that the use of public information is not likely to promote group foraging by itself, which is in agreement with Sernland et al (2003). However, for individuals which already forage in groups, for example because of a high predation risk, sharing public information may offer yet another advantage to being in such a group.

Figure 3.1 - Example plots showing the initial number of prey (X) occurring in a series of 500 patches, according to a negative binomial distribution, with the mean number of prey per patch = 150. **(a)** Parameter values: $\lambda = 500$, $\alpha = 0.3$, variance = 195 (as suggested by Valone, 1993). **(b)** Parameter values $\lambda = 6$, $\alpha = 25$, variance = 3900.

(a)



(b)

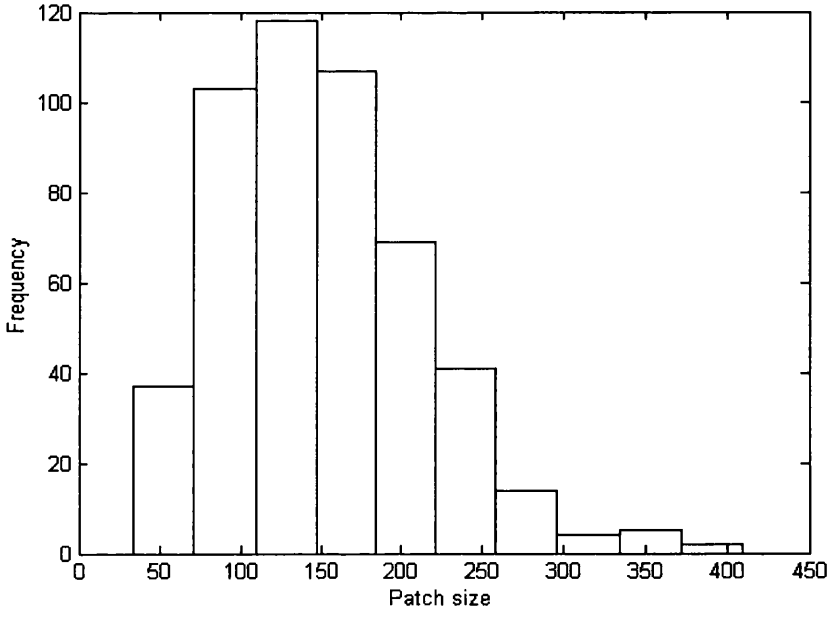
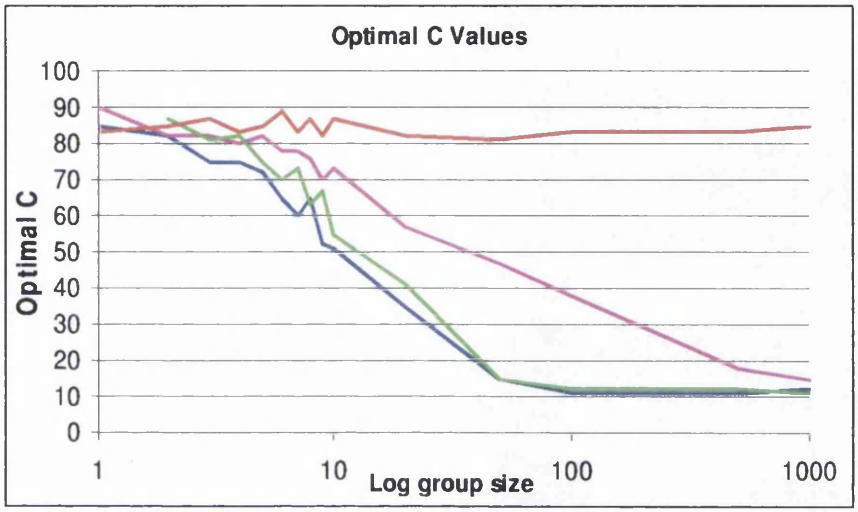


Figure 3.2 - Optimal values of C obtained for prey distribution environments with a mean = 250 prey items per patch **(a)** variance = 2750; **(b)** variance = 5250; **(c)** variance = 8062.5. Legend: red = Totalinfo; blue = First; pink = Leader; green = Paired.

(a)



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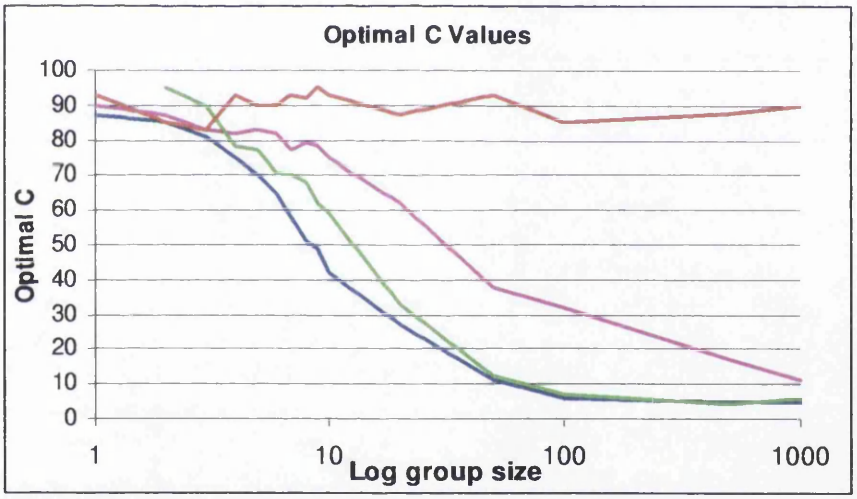

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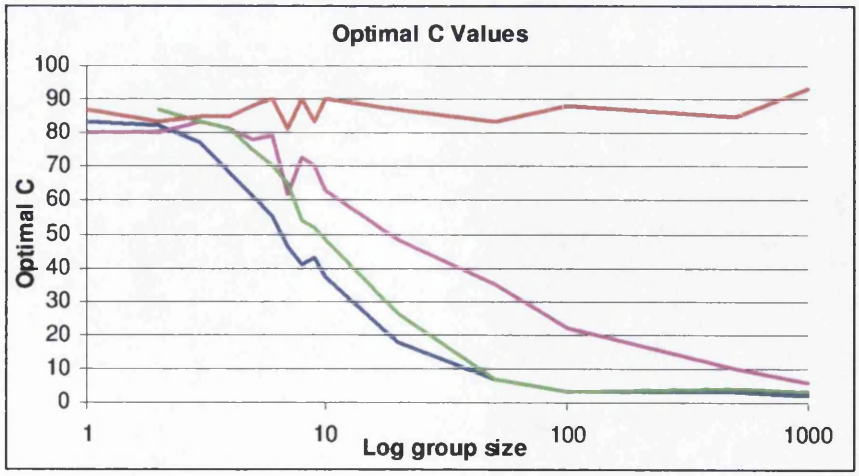


Figure 3.3 - Prey capture rates for First strategy using optimal C values obtained by groups using the First strategy (--●--), and for the 'perfect optimal' C values obtained for Totalinfo strategy (--o--). Also displayed are the capture rates for Totalinfo groups using 'perfect' optimal C values obtained by Totalinfo strategy (--x--). Mean = 250, variance = 8062.5.

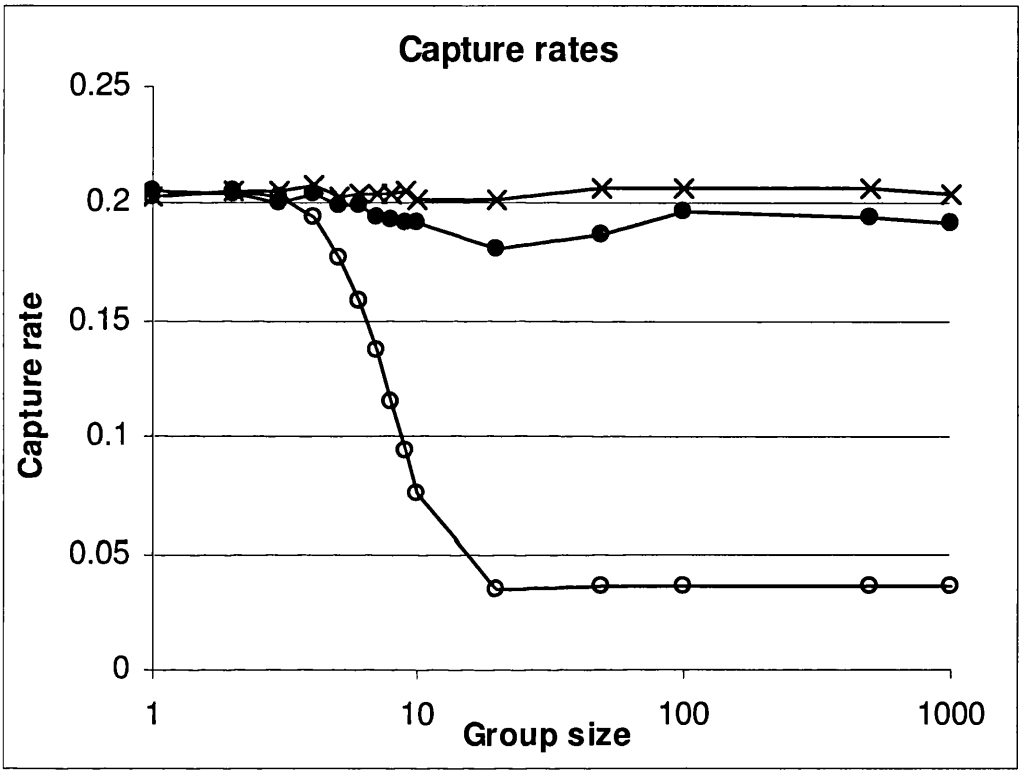
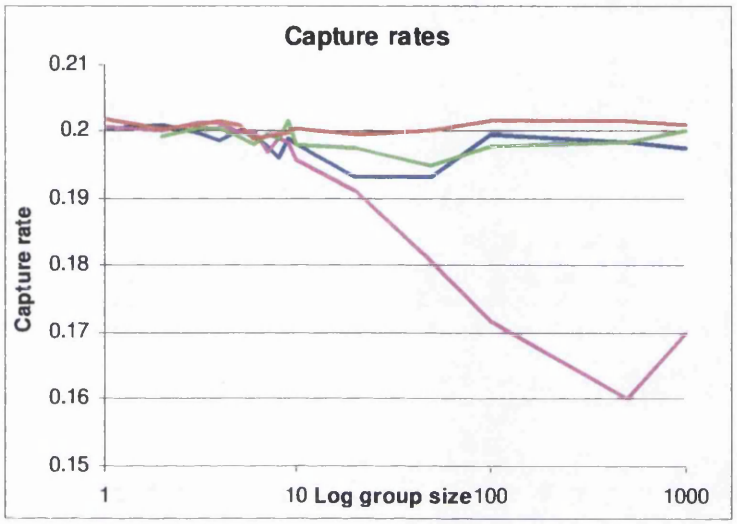
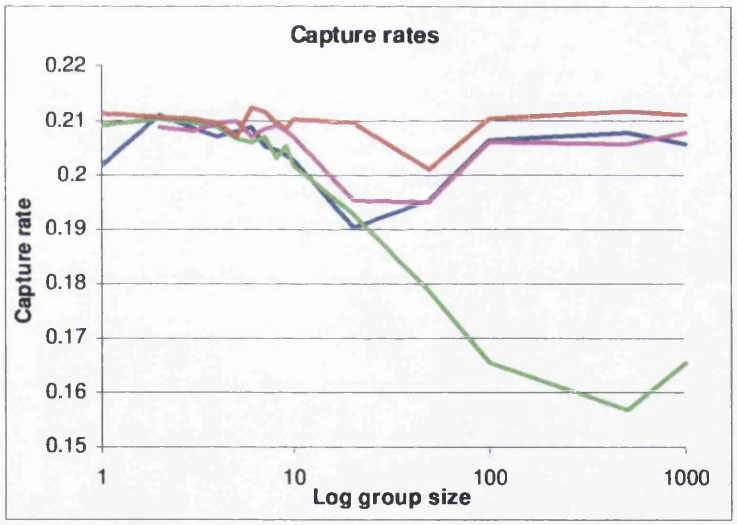


Figure 3.4 - Prey capture rates obtained by foraging groups using three patch quitting strategies and for groups sharing public information, in prey distribution environments with a mean = 250 prey items per patch: (a) variance = 2750; (b) variance = 5250; (c) variance = 8062.5. Legend: red = Totalinfo; blue = First; green = Leader; pink = Paired.

(a)



(b)



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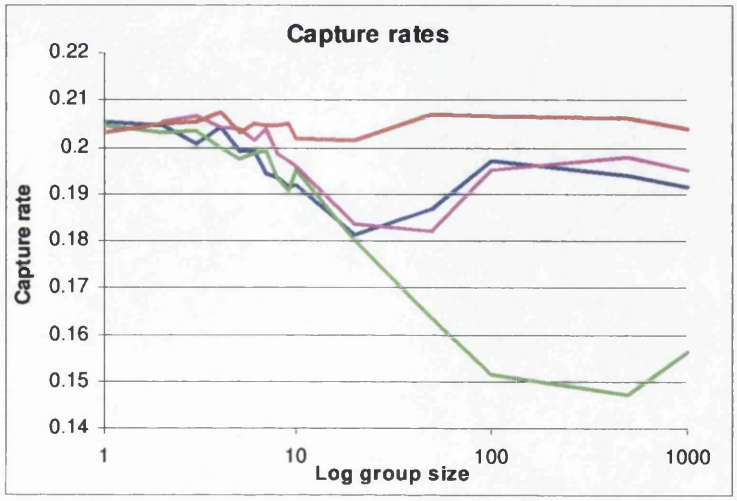
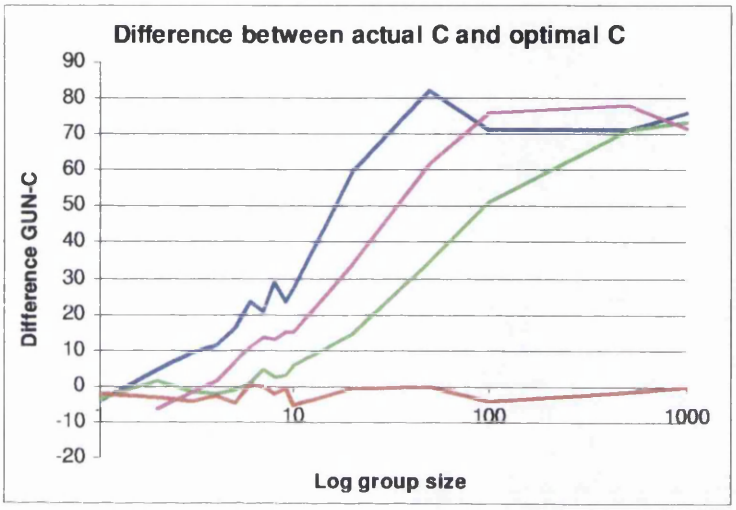
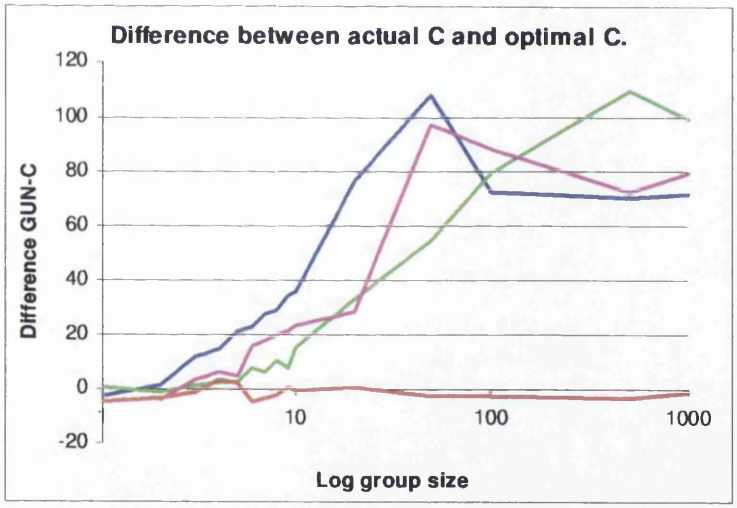


Figure 3.5 - Difference obtained by subtracting the optimal value of C from the actual quitting value of C, by foraging groups using three patch quitting strategies and for groups sharing public information, in prey distribution environment with a mean = 250 prey items per patch: **(a)** variance = 2750; **(b)** variance = 5250; **(c)** variance = 8062.5. Legend: red = Totalinfo; blue = First; green = Leader; pink = Paired.

(a)



(b)



(c)

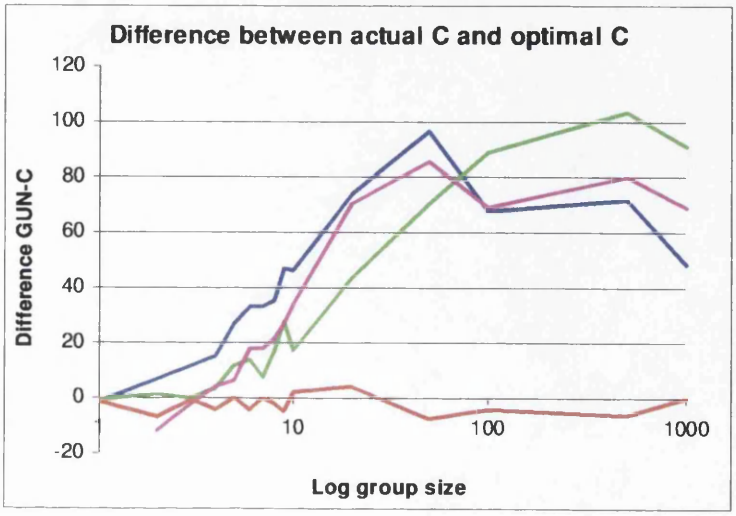
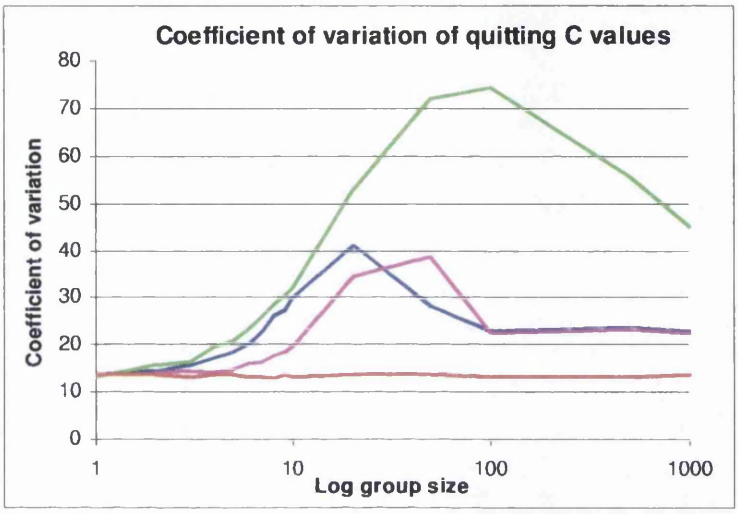
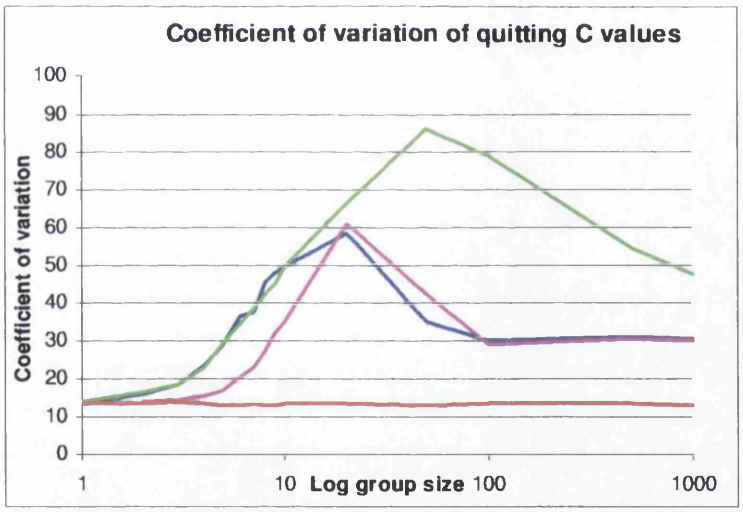


Figure 3.6 - Coefficient of variation of the quitting value of C obtained by foraging groups using three patch quitting strategies and for groups sharing public information, in prey distribution environments with a mean = 250 prey items per patch: **(a)** variance = 2750; **(b)** variance = 5250; **(c)** variance = 8062.5. Legend: red = Totalinfo; blue = First; green = Leader; pink = Paired.

(a)



(b)



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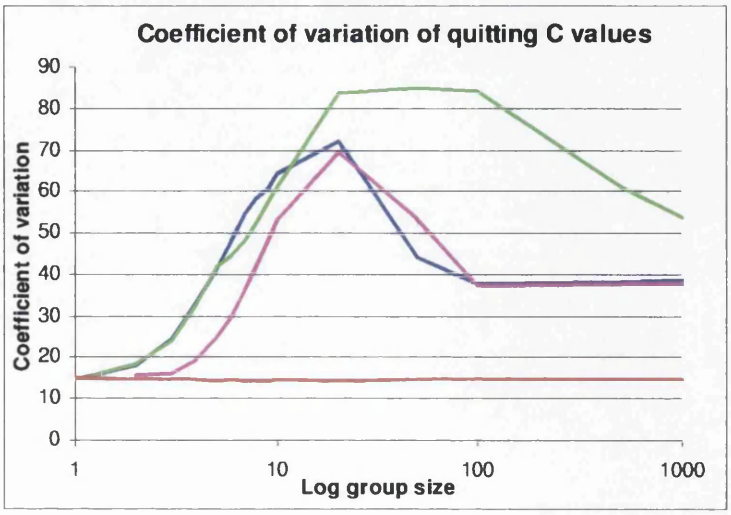


CHAPTER 4

PATCH ESTIMATION IN LARGE GROUPS – AN UNBIASED VERSION OF IWASA ET AL'S (1981) PATCH DEPLETION MODEL

ABSTRACT

Animals feeding in an uncertain environment must somehow estimate the quality of the food patches they visit, in order to maximise long-term prey intake rates. Iwasa et al (1981) developed a formula which models the estimation of prey depletion within a patch, as a forager feeds there. The formula requires only details of the prey distribution across the environment, the amount of time spent feeding in a patch, and the number of prey items found in that time. For animals feeding in large groups this model can be modified so that each forager projects its own foraging success onto every other forager in the group, in order to estimate the total number of prey found by the group as a whole. In large groups this is unrealistic, since each forager stands a lesser chance of finding prey. In this chapter I present a model that removes this bias by taking into account the number of search attempts made by the group. I show that in small groups both models yield similarly accurate estimates of patch quality, whilst in larger groups of foragers the model presented here produces significantly more accurate estimates, on average. However there is also a much higher variation in prey estimation from patch to patch, and so overall foragers simuated with this model do not always experience an increased long-term foraging success.

INTRODUCTION

In an attempt to investigate the optimal patch-quitting behaviour of a lone forager moving between a series of depleting food patches, Iwasa et al (1981) described a formula which generates an estimate of the number of food items remaining in each food patch, based upon how much time (t) a forager has spent in a particular patch and how many prey items (n) it has found in that time. This estimator, shown in equation (1), is able to calculate with some level of accuracy the number of prey items that remain in a patch:

$$E\ (n,t) = \frac{\lambda + n}{\left(\exp(At)\left(\frac{\alpha+1}{\alpha}\right) - 1\right)} \qquad (1)$$

where A = the searching rate (the fraction of the patch searched per unit time) and λ,α are parameters of the negative binomial distribution describing the prey environment.

In the previous chapter we modify this model to investigate animals feeding in cohesive groups. A forager does not know how well each other individual is doing, and so can only estimate group foraging success by assuming that all other foragers are experiencing the same success as itself. The formula takes the number of prey found by each individual in the group and multiplies it by the number of foragers in the group, and simply becomes

$$E_{i,N}(n,t) = \frac{\lambda + Nn_i}{\exp\left(\frac{NS_1 t}{p}\right)\left(\frac{\alpha+1}{\alpha}\right) - 1} \qquad (2)$$

where N = the number of individuals in the group, and S_1 = the individual search rate.

This assumption appears a sensible one for small groups and is easy to implement; however, the estimator described in equation (2) is likely to be unrealistic for large groups. As the group size increases, the estimate of any one individual is likely to become progressively more inaccurate because it will become less and less likely that all foragers will find prey on every search attempt. For example, if a group contains

100 individuals, a forager finding one prey item will assume that each of the other 99 individuals has also found prey. Similarly, if it does not find a prey item it assumes that all other group members have not found prey. The estimator will thus consistently overpredict the number of prey items in the patch if it has caught a lot of prey, and underpredict the number of prey it it has caught a few items, so that given the number of prey items caught the estimator will be biased. This assumption will lead to vastly different and wildly inaccurate patch estimates, and may encourage the group to quit patches before it is beneficial for them to do so. It becomes an even greater problem when we consider very large groups, where the number of individuals present in a patch may outnumber the available prey resources.

It is true that as group size increases a patch will be depleted relatively more quickly, as in larger groups it is more likely that prey will be found on each turn. However, it also becomes more unlikely that any particular individual will actually find a prey item because there are so many other foragers that may have found it instead. The bias produced by the model described in equation (2) will thus affect the accuracy of the estimate that any forager can make as to how many prey remain in a patch, and particularly so in large groups. Here we attempt to rectify this problem and present a modified version of the group foraging estimator (eq. 2). We do this by removing the assumption inferred by the previous model that prey discovery is equaly likely at all times. We take into account the effect of patch depletion on the future likelihood of prey discovery and the reduced success of sampling by each individual both as the patch becomes depleted and as group size increases.

MODEL DESCRIPTION

We begin by considering the probability of a given number of prey items being initially present in a patch. This is described by the negative binomial

$$\binom{n+k+\lambda-1}{n+k}\left(\frac{1}{1+\alpha}\right)^{\lambda}\left(\frac{\alpha}{1+\alpha}\right)^{n+k} \qquad (3)$$

where the total number of prey in a patch, m, is the sum of the number found (n) and the number remaining (k), and where m is defined by the negative binomial parameters λ,α as in the previous model.

The probability of n prey items out of m=n+k being found by time t is given by

$$\binom{n+k}{n}\left(e^{-NSt}\right)^{k}\left(1-e^{-NSt}\right)^{n} \tag{4}$$

where N is the number foragers in the group and S is the individual search rate of each forager (all foragers search a patch at an equal rate). The probability of any particular forager finding n_1 of these prey, given that n have been found, is given by $\binom{n}{n_1}\left(\frac{1}{N}\right)^{n_1}\left(1-\frac{1}{N}\right)^{n-n_1}$ and so combining equations (3) and (4) gives the probability of one forager finding n_1 prey, where n prey have been found by time t in total:

$$\binom{n+k}{n}\left(e^{-NSt}\right)^{k}\left(1-e^{-NSt}\right)^{n}\binom{n}{n_1}\left(\frac{1}{N}\right)^{n_1}\left(1-\frac{1}{N}\right)^{n-n_1}. \tag{5}$$

Thus, the probability of there being k prey remaining in a patch, and n items have been found by time t, of which n_1 have been found by one forager is

$$\binom{n+k+\lambda-1}{n+k}\left(\frac{1}{1+\alpha}\right)^{\lambda}\left(\frac{\alpha}{1+\alpha}\right)^{n+k}\binom{n+k}{n}\left(e^{-NSt}\right)^{k}\left(1-e^{-NSt}\right)^{n}\binom{n}{n_1}\left(\frac{1}{N}\right)^{n_1}\left(1-\frac{1}{N}\right)^{n-n_1} \tag{6}$$

It follows that

P[k items remain in a patch, and one forager has found n_1 items by time t] =

$\sum_{n}$ P[n+k items in a patch, if the group has found n by time t, n_1 of which were found by one forager]

This can be expanded so that

$$\sum_{n}\frac{n+k+\lambda-1!}{(n+k)!(\lambda-1)!}\frac{n+k!}{n!k!}\frac{n!}{n_1!n-n_1!}\left(\frac{1}{1+\alpha}\right)^{\lambda}\left(\frac{\alpha}{1+\alpha}\right)^{n}\left(\frac{\alpha}{1+\alpha}\right)^{k}\left(e^{-NSt}\right)^{k}\left(1-e^{-NSt}\right)^{n}\left(\frac{1}{N}\right)^{n_1}\left(1-\frac{1}{N}\right)^{n}\left(1-\frac{1}{N}\right)^{-n_1}$$

$$=\sum_{n}\frac{n+k+\lambda-1!}{n-n_1!}\frac{n_1+k+\lambda-1!}{n_1+k+\lambda-1!}\frac{1}{(\lambda-1)k!n_1!}\left(\frac{\alpha}{1+\alpha}\left(1-e^{-NSt}\right)\left(1-\frac{1}{N}\right)\right)^{n}\left(\left(\frac{1}{1+\alpha}\right)^{\lambda}\left(\frac{\alpha}{1+\alpha}\right)^{k}\left(e^{-NSt}\right)^{k}\left(\frac{1}{N}\right)^{n_1}\left(1-\frac{1}{N}\right)^{-n_1}\right) \tag{7}$$

Where $\frac{\alpha'}{1+\alpha'} = \left(1-e^{-NSt}\right)\frac{\alpha}{1+\alpha}\left(1-\frac{1}{N}\right)$ this becomes

$$\sum_n \binom{n+k+\lambda-1}{n-n_1}\left(\frac{\alpha'}{1+\alpha'}\right)^{n-n_1}\left(\frac{1}{1+\alpha'}\right)^{n_1+k+\lambda}\left((1+\alpha')^{n_1+k+\lambda}\frac{n_1+k+\lambda-1!}{n_1+k+\lambda-1!}\left(\frac{1}{1+\alpha}\right)^{\lambda}\left(\frac{\alpha}{1+\alpha}\right)^{k}\left(e^{-NSt}\right)^{k}\left(1-e^{-NSt}\right)^{n_1}\left(\frac{1}{N}\right)^{n}\right)$$

$$=(1+\alpha')^{n_1+k+\lambda}\frac{n_1+k+\lambda-1!}{\lambda-1!k!n_1!}\left(\frac{1}{1+\alpha}\right)^{\lambda}\left(\frac{\alpha}{1+\alpha}\right)^{k}\left(e^{-NSt}\right)^{k}\left(1-e^{-NSt}\right)^{n_1}\left(\frac{1}{N}\right)^{n_1}$$

$$=\frac{n_1+k+\lambda-1!}{\lambda-1!k!n_1!}\frac{n_1+\lambda-1!}{n_1+\lambda-1!}(1+\alpha')^{k}\left(\frac{\alpha}{1+\alpha}\right)^{k}\left(e^{-NSt}\right)^{k}(1+\alpha')^{n_1+\lambda}\left(\frac{1}{N}\right)^{n_1}\left(\frac{1}{1+\alpha}\right)^{\lambda}\left(1-e^{-NSt}\right)^{n_1}\left(\frac{\alpha}{1+\alpha}\right)^{n_1} \tag{8}$$

And where $\frac{\beta'}{\beta'+1} = (1+\alpha')\frac{\alpha}{1+\alpha}e^{-NSt}$

$$\propto \binom{n_1+k+\lambda-1}{k}\left(\frac{\beta'}{\beta'+1}\right)^{k}\left(\frac{1}{1+\beta'}\right)^{n_1+\lambda}. \tag{9}$$

So the predictor $r(n_1,t) = (n_1+\lambda)\beta'$.

We now rearrange

$$\alpha' = \left(1-e^{-NSt}\right)\frac{\alpha}{1+\alpha}\left(1-\frac{1}{N}\right)+\alpha'\left(1-e^{-NSt}\right)\frac{\alpha}{1+\alpha}\left(1-\frac{1}{N}\right)$$

to give

$$\Rightarrow \alpha' = \frac{\left(1-e^{-NSt}\right)\frac{\alpha}{1+\alpha}\frac{N-1}{N}}{1-\left(1-e^{-NSt}\right)\frac{\alpha}{1+\alpha}\frac{N-1}{N}}$$

$$\Rightarrow 1+\alpha' = \frac{1}{1-\left(1-e^{-NSt}\right)\frac{\alpha}{1+\alpha}\frac{N-1}{N}} \tag{10}$$

Similarly, we rearrange

$$\Rightarrow \frac{\beta'}{1+\beta'} = \frac{\alpha}{1+\alpha}\frac{e^{-NSt}}{1-\left(1-e^{-NSt}\right)\frac{\alpha}{1+\alpha}\frac{N-1}{N}}$$

$$= \frac{1}{\frac{1+\alpha}{\alpha}e^{NSt}-\frac{N-1}{N}\left(e^{NSt}-1\right)} \tag{11}$$

$$\Rightarrow \beta'\left(\frac{1+\alpha}{\alpha}e^{NSt}-\frac{N-1}{N}\left(e^{NSt}-1\right)\right)=1+\beta'$$

$$\Rightarrow \beta'=\frac{1}{\frac{1+\alpha}{\alpha}e^{NSt}-1-\frac{N-1}{N}\left(e^{NSt}-1\right)} \tag{12}$$

$$=\frac{1}{\frac{1+\alpha}{\alpha}e^{NSt}-\frac{N-1}{N}e^{NSt}-\frac{1}{N}}$$

$$=\frac{1}{-\frac{1}{N}+e^{NSt}\frac{1}{\alpha N}(N+\alpha)}$$

$$=\frac{\alpha N}{-\alpha+e^{NSt}(N+\alpha)} \tag{13}$$

And so the new estimator, taking into account bias caused by extreme group sizes, is

$$\Rightarrow r(n_1 t)=\frac{(\lambda+n_1)\alpha N}{(N+\alpha)e^{NSt}-\alpha}$$

$$=\frac{(\lambda+n_1)N}{\frac{N+\alpha}{\alpha}e^{NSt}-1}. \tag{14}$$

Figure 4.1 shows the estimates for the remaining number of prey in a patch by foragers as they feed, generated by the original group foraging estimator shown in equation (2) and the new group-size-corrected estimator in equation (14). While group size is small there is little difference between models. The estimation of remaining prey number decreases in both models, following the depletion of prey. But as group size increases the group-size-corrected model produces estimates that are considerably higher after a given time spent in a patch than those in the original function. The individual modelled with the original group foraging function assumes that each other individual has taken the same number of prey as itself, so in large groups it estimates that the patch is being depleted very rapidly. The individual modelled using the group-size-corrected function takes into account this unrealistic assumption and does not over-estimate patch depletion to the same extent.

Using the above formulation (equation 14), we repeated the simulations performed in the previous chapter. To minimise computational time we used the same optimal values of C that were obtained from those trials. Each simulation was carried out over a series of 500 patches, and each simulation was repeated 2000 times.

RESULTS

Patch estimation with no public information use

Prey capture rates - In these simulations, there is little difference in capture rates between models when group size remains low (Figure 4.2a, b, c). For all three strategies (First, Leader and Paired) the foraging success of individuals in groups up to a size of about 10 foragers is not noticeably different from that of a lone forager, using either model. In larger groups, the prey capture rate begins to decline, and we also see differences between the two estimator models.

Groups using the First strategy (Figure 4.2a) experience a slight overall decrease in capture rate using the group-size-corrected model as group size increases, whereas there is a considerable decrease using the original group foraging model. In the largest groups (N = 1000) individuals in the original group model see capture rates half those of the size-bias group model. For the Leader strategy (Figure 4.2b), both models see a decline in capture rates in groups containing more than 10 individuals. Capture rates remain slightly, but consistently higher for Leader groups using the size-corrected model, in all except the largest groups. Looking at the Paired strategy (Figure 4.2c), groups containing fewer that 10 individuals experience prey capture rates that are similar for both versions of the model. Both see a slight decline as group size reaches 20 individuals, but as group size continues to increase the capture rate with the size-biased model decreases further, while the original estimator levels off and almost recovers its original value in the largest groups – the size-corrected model being almost half this value.

The important result here is that using a method of patch estimation which takes into account the effects of extreme group size, as described in equation (14), does not

improve prey capture rates for any of the groups not sharing public information. This is surprising because this is the opposite of what we would intuitively predict. In smaller groups there is a slight increase in capture rates over the same strategies using the unmodified estimator, but larger groups in fact fare worse than those adopting the (perhaps simpler) method of patch estimation described in equation (2).

Quitting patches at optimal C - In all simulations using the modified group-size-corrected model, each of the strategies were better able to quit patches at the optimal value of C than when using the original group foraging model (Figure 4.3a, b, c). Both First and Paired groups only ever over- or under-utilised patches by a few prey items (Figure 4.3a, c). Groups adopting the Leader strategy with the group size-bias model were able to quit patches almost perfectly close to the optimal value of C (Figure 4.3b), since the difference between optimal C and the GUN is close to 0 in all simulations. Using the original group foraging model, each of these groups quit the patch progressively earlier as group size increased. This heavily implies that the new group size-biased estimator model is more effective than the previous group foraging estimator.

Despite the impressive overall ability of these groups to quit patches at the optimal value of C using this new model, they are still rarely more successful than when using the original group foraging model. This is particularly the case in large groups – which is opposite to what we predicted. To understand this we must look at Figure 4.4. Figure 4.4 shows the coefficient of variation of quitting C (GUN) values for each of these group patch quitting strategies. We can see that all three strategies have low CoV values whilst in groups containing fewer than 20 individuals – this suggests that they are able to accurately estimate and quit patches close to the optimal level of C, on a consistent basis. However, as group size rises above 20, CoV increases dramatically in all three groups. Although the new size-biased model is able to make an accurate estimate of C on average, it is not able to do so consistently. In large groups the patch quitting value becomes extremely erratic - in the largest groups, this is in fact worse than when using the original estimator.

This sharp increase in CoV can adequately explain why the overall foraging success (prey capture rate) of groups simulated with this model is in most cases not beneficial

over groups simulated using the original model. In small groups we do not expect to see any difference in foraging success, since the size-biased estimator is only intended to have an effect on large groups. Small groups should not be subject to the same problems in estimation as large groups. In large groups the new estimator *does* achieve the desired effect – it clearly enables groups of each strategy to quit patches closer to the optimal value of C. But it does not do so on a consistent basis. This leads to a very inefficient use of the available foraging time.

This is perhaps what we should expect to see. The Leader strategy quits patches only taking into account the foraging success of one individual, which remains the same from patch to patch. This leader individual will therefore tend, on average, to quit patches at the correct time, regardless of group size. Sometimes it will have the highest patch estimate, and sometimes the lowest, so its estimate will on average represent the true prey quality of the patch. The improved formula presented here enables each individual in a group to make a more accurate estimate of patch quality. Bearing these two points in mind, we should expect the groups to quit on average closer to the optimal value of C than in the previous model. However, because the leader individual will have the correct estimate of patch quality only on average, and will also experience estimates at either extreme of the distribution, the actual quitting value of C will be quite variable, demonstrated by the high correlation of variation.

In the First and Paired groups, this problem is reduced somewhat. The new model is designed to reduce the dissimilarity between estimates, the group will still hold a distribution of estimates between them, albeit a narrower one than before. The First and Paired strategy quit patches with the individuals that are experiencing the lowest patch estimate, so this continues to be sensitive to bad luck due to the stochastic nature of foraging. They will never be able to quit patches close to optimal C all the time – they will always tend to quit too early. The coefficient of variation in quitting value of C for both First and Paired strategies are almost identical (Figure 4.4), and increase with group size for both of these groups. Although groups using these strategies manage to quit patches (on average) close to the optimal value of C, they become less consistent as the number of individuals in a group grows. In the largest groups this is considerably higher than for groups using the original group foraging model.

It is interesting to note that in all simulations the quitting value of C for groups using the Paired strategy is lower than for the First strategy. This lends further support to Ruxton's (1995b) theory that groups can minimise the risk of leaving too early if they wait for two foragers to agree on when to quit a patch, rather than leaving with the first individual.

DISCUSSION

In previous simulations we examined a method by which foragers could estimate the number of prey items remaining in a depleting patch of food, where information relating to prey capture events is not shared among all members of a group. Each individual makes its patch estimate depending solely upon its own foraging success, i.e. by assuming that each other forager in the group has had the same success as itself. But in large groups this is likely to be an unrealistic assumption, and here we have considered another model that takes into account the effects of extreme group sizes on this estimate.

The results obtained here show that using this group-size-corrected estimator does indeed enable individuals in larger groups to make more accurate patch estimates of remaining patch quality, in comparison with the previous estimator. All three strategies (First, Leader and Paired) were able to quit patches closer to the optimal value of C than in previous simulations. In particular, the largest groups, which became progressively worse at accurately estimating patch quality and thus quitting patches earlier with increasing group size when modelled using the original group foraging estimator (equation 2), were much better able to quit patches at optimal value of C using the modified group size-bias estimator (equation 12). In none of the simulations did any of these groups quit patches more than 15 prey items too early, and in most cases they did not quit more than 10 items too early, in comparison with a value as high as 80 in the previous simulations. However, the coefficient of variation for quitting values of C increased severely with group size using this model, and so despite being able to quit patches more accurately *on average*, they became less consistent at doing so overall.

We concluded in Chapter 3 that the largest groups were able to quit patches close to the optimal value of C because they were depleting the patches much faster than smaller groups and also leaving almost immediately. Due to the sensitive nature of the First and Paired strategies to runs of bad luck and poor patch quality (Valone, 1993; Ruxton, 1995b) - i.e. they were quitting patches at 'the first sign of trouble' - these groups were actually seeing benefits because the patches were becoming poor very quickly. For example, a group of 1000 individuals would leave a patch almost immediately, because as soon as one forager had found a prey item because it would assume that the other 999 had also done so and the patch must now be entirely empty. Although it wasn't necessarily true that all 1000 individuals had found prey, it was entirely likely that enough individuals had found prey so that the patch was now empty, or very poor. Staying longer would be detrimental, because it could not possibly be profitable. Quitting with the individual with the lowest estimate (First strategy) therefore helped to ensure that this did not happen. Paired groups did not do so well under the same circumstances because they did not leave at the 'first sign of trouble' but at 'the second sign of trouble' – i.e. when another individual agreed that the patch was poor. They stayed in the patch slightly longer and wasted time in an unprofitable patch.

Although these groups quit patches with the lowest individual estimates (First and Paired strategies), the group quit patches incredibly early - but they also did so fairly consistently. The large groups always quit patches when they had been exhausted to a similar extent – more than likely it had been totally exhausted and was now empty. Using the group-size-corrected model each forager now weights its estimate against large groups. The result may be that each forager has a more accurate estimate of patch quality, but the advantage of increased sensitivity to sudden patch depletion is now lost, and the quitting value of C in the non-information sharing groups becomes much more variable. The capture rates of such groups suffer because of this. In such large groups remaining in a patch slightly too long, or quitting slightly too early may have a huge effect on capture rates, since the total time wasted is much greater than in smaller groups.

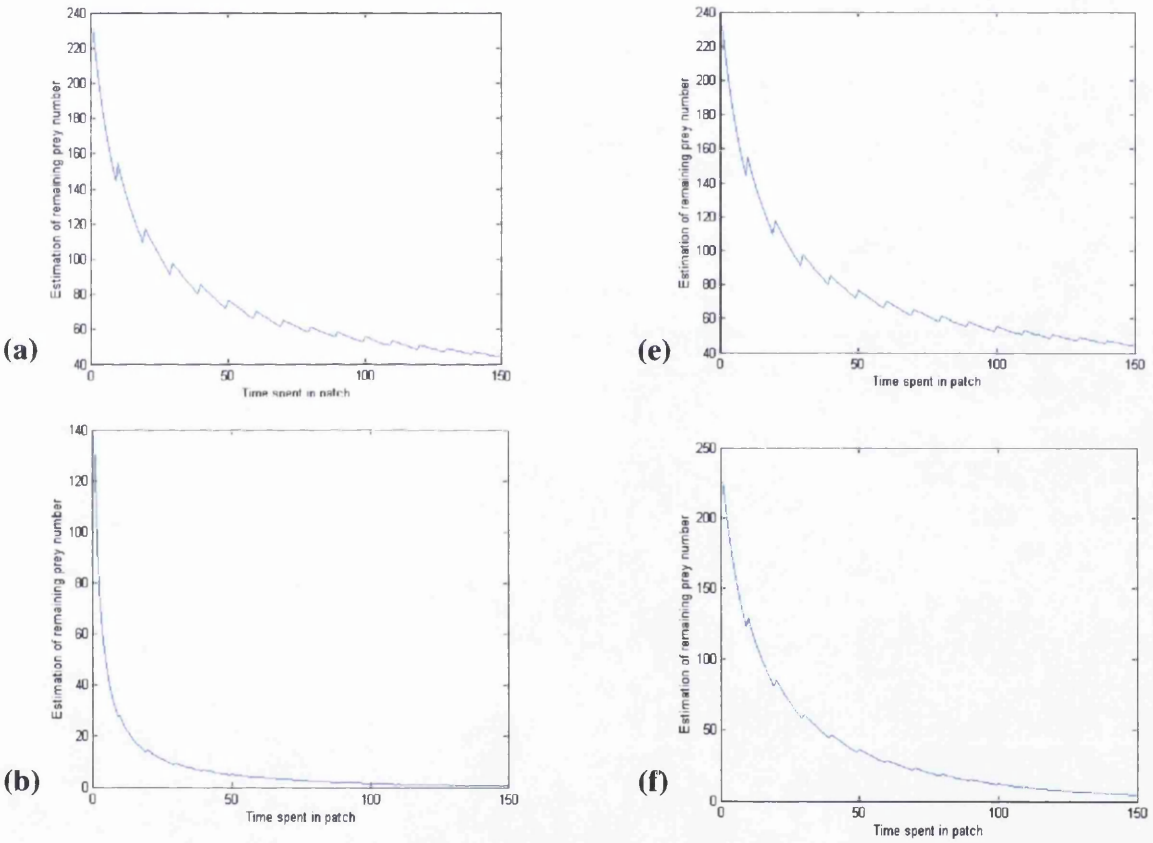
In our modified group size-biased formula, the estimator uses a way of estimating how many prey have been found between all members of the group, and all

individuals share a more similar estimate of patch quality. However, because all estimates are now so similar, if one individual is incorrect, it is likely that all other individuals are also incorrect. This works fine for the Leader strategy, because this strategy relies upon the foraging success of one specified individual, and ignores that of the other group members. On an individual level, this estimator is favourable over the previous group foraging model. The estimate is likely to average out so that the quitting C falls close to the optimal C – although as we have seen this is very inconsistent. First and Paired groups still rely on the estimate of *any* individual, so this is vulnerable to error made by the whole group – this is particularly likely where variation in the number of prey between patches is high, or where group size is very large.

FUTURE WORK

One of the biggest assumptions made in this, and other models of public information theory (Clark and Mangel, 1984, 1986; Valone 1993; Ruxton, 1995b) is that there is no cost to the sharing of public information. This is probably an unlikely and unrealistic assumption to make for animals foraging in the wild (Templeton and Giraldeau, 1995b; Desimone and Duncan, 1995; Dukas and Kamil, 2000; Dukas, 2002; Dukas and Ellner, 2003; Clark and Dukas, 2003). Foragers would almost certainly incur some cost to sharing public information. Firstly there may be some metabolic cost to transmitting a prey capture signal. Similarly, there will probably be a cost in receiving these signals, either through a loss in personal foraging time due to attentional limitations (i.e. concentrating less on immediate foraging activity in order to place more attention on the prey capture signals of others) but also through mistaken or missed signals – incorrectly interpreting something as a signal when there wasn't one, or totally missing a true signal altogether. This is particularly plausible in large groups, where a forager has to interpret the actions of many more individuals, and of course there is a much higher chance of interference from others. Here, and in previous work (see Chapter 4), we showed that the sharing of public information is only really beneficial in larger groups when there is no cost associated with it. The next question to be answered then, should be 'is this still the case when public information is not cost free?'

Figure 4.1 - Plots comparing estimations of the remaining number of prey in a patch over time, using a version of Iwasa et al's (1981) estimator function modified for group foragers (equation 2) for groups containing **(a)** one individual, **(b)** 10 individuals, **(c)** 100 individuals, **(d)** 1000 individuals; and our estimator function modified for extreme group sizes (equation 11), for groups containing **(e)** one individual, **(f)** 10 individuals, **(g)** 100 individuals, **(h)** 1000 individuals. $\lambda = 8$, $\alpha = 31.25$.



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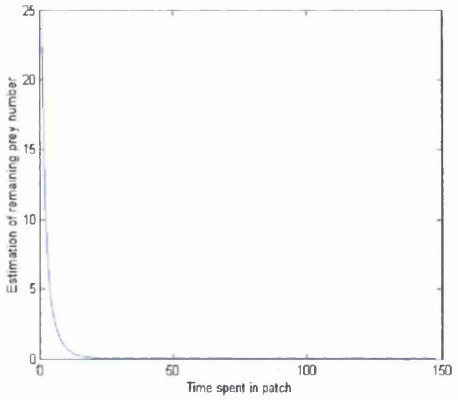
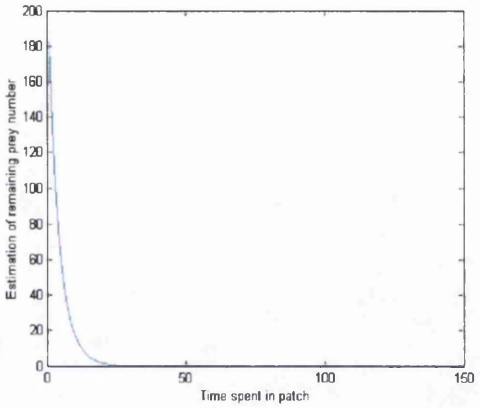
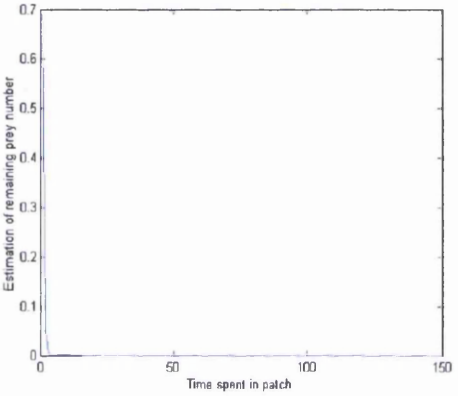

Estimation of remaining prey number
Time spent in patch
0
5
10
15
20
25
0
50
100
150

(g)


Estimation of remaining prey number
Time spent in patch
0
20
40
60
80
100
120
140
160
180
200
0
50
100
150

(d)


Estimation of remaining prey number
Time spent in patch
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0
50
100
150

(h)

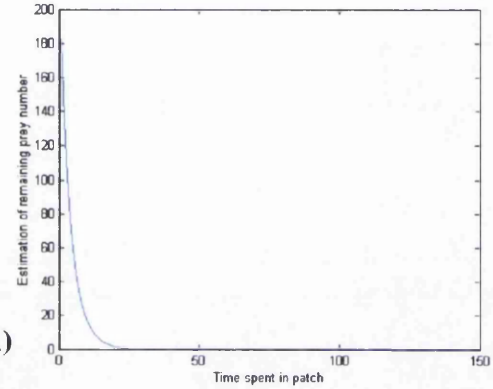
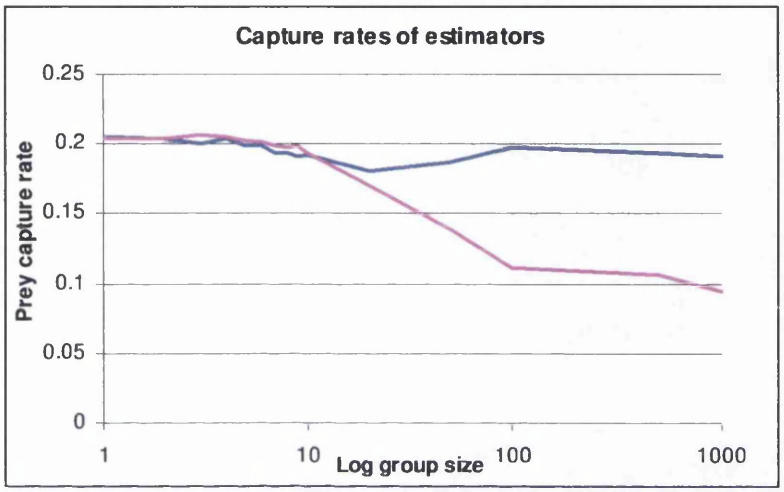
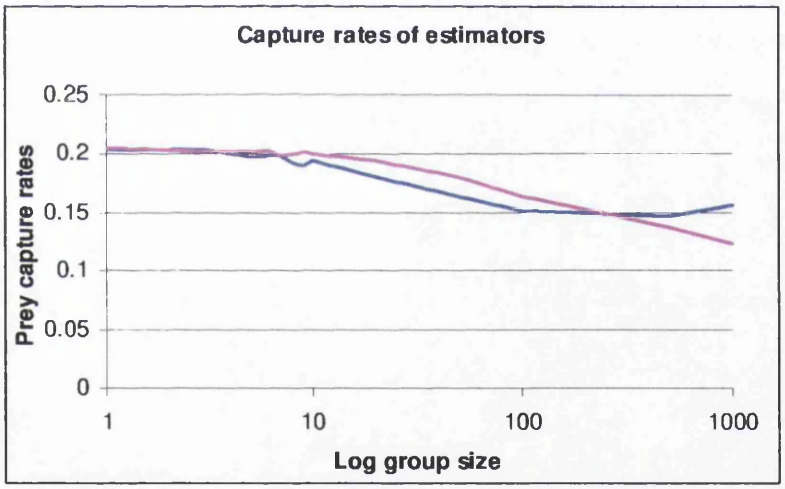

Estimation of remaining prey number
Time spent in patch
0
20
40
60
80
100
120
140
160
180
200
0
50
100
150

Figure 4.2 - Prey capture rates obtained by foraging groups using the modified group size corrected estimator model, and the original group foraging model, by foragers using three non information sharing patch quitting strategies: **(a)** First, **(b)** Leader, **(c)** Paired. Mean number of prey per patch = 250, variance = 8062.5. Original estimator - blue, group size corrected estimator - pink.

(a)



(b)



(c)

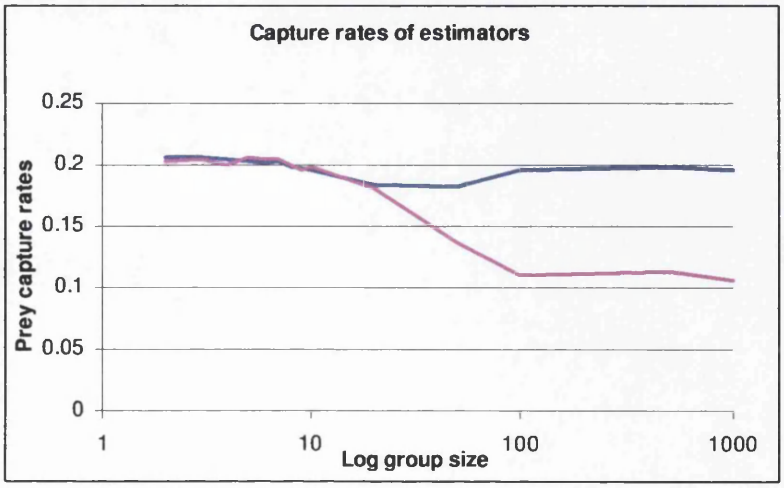
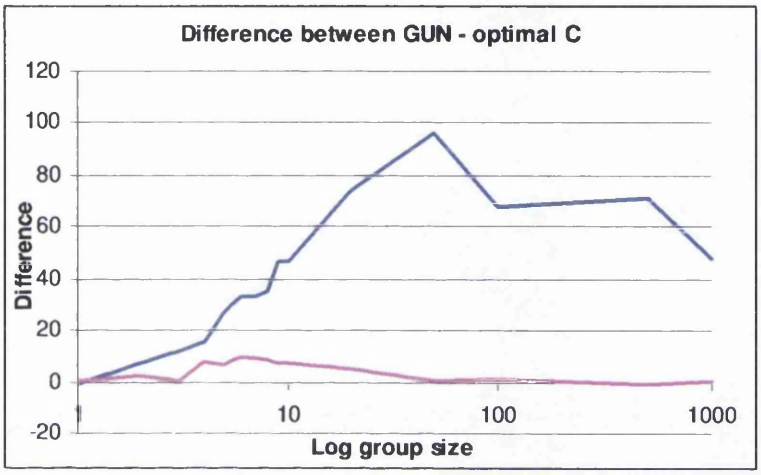
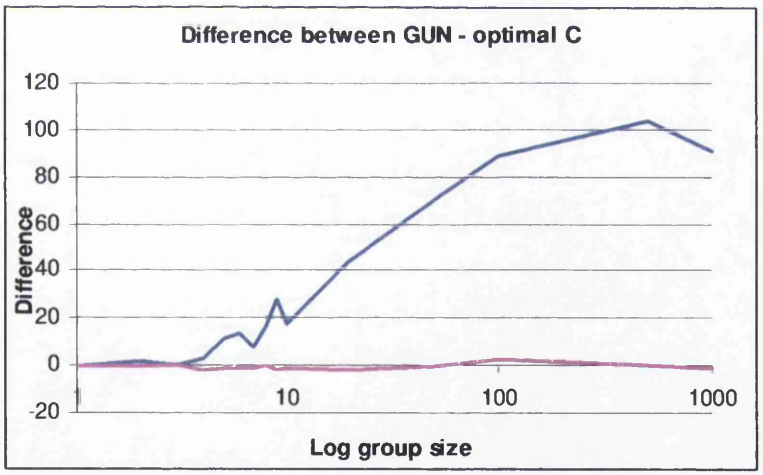


Figure 4.3 - Difference between actual quitting value of C (GUN) and optimal value of C, obtained by group foragers using the modified group size corrected estimator model, and the original group foraging model, by foragers using three non information sharing patch quitting strategies: **(a)** First, **(b)** Leader, **(c)** Paired. Mean number of prey per patch = 250, variance = 8062.5. Original estimator - blue, group size corrected estimator - pink.

(a)



(b)



(c)

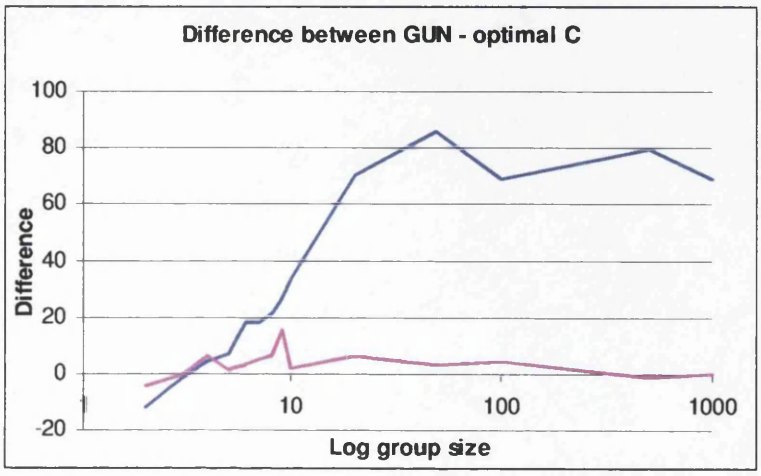
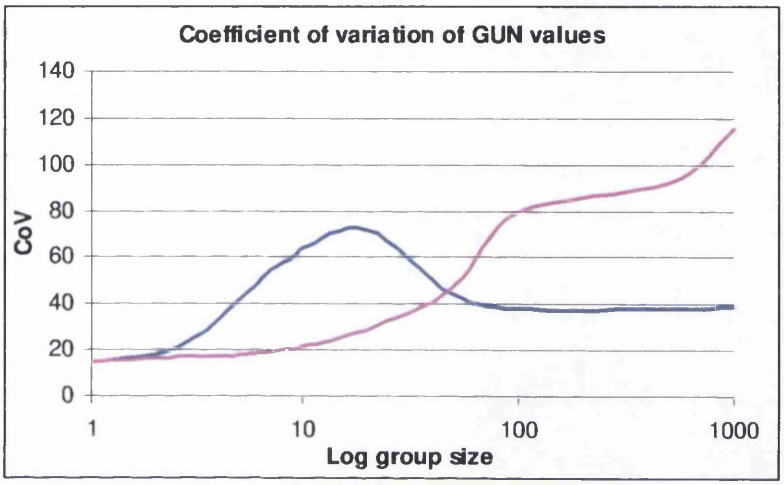
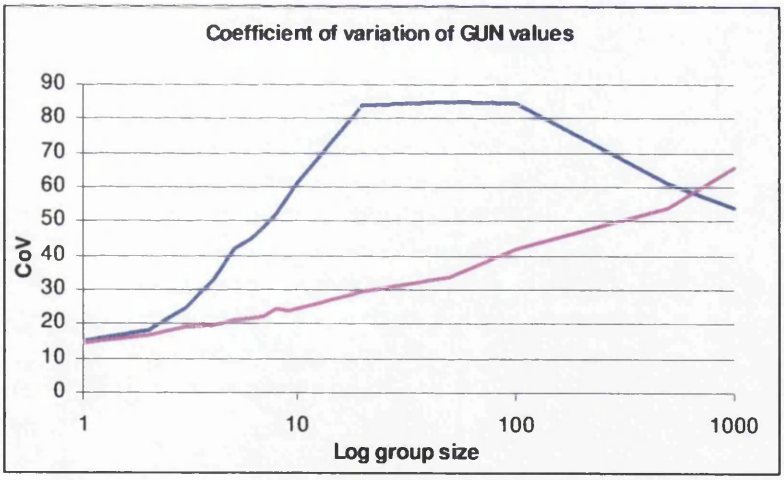


Figure 4.4 a, b, c - Coefficient of variation of patch quitting value of C (GUN), obtained by group foragers using the modified group size corrected estimator model, and the original group foraging model, by foragers using three non information sharing patch quitting strategies: **(a)** First, **(b)** Leader, **(c)** Paired. Mean number of prey per patch = 250, variance = 8062.5. Original estimator - blue, group size corrected estimator - pink.

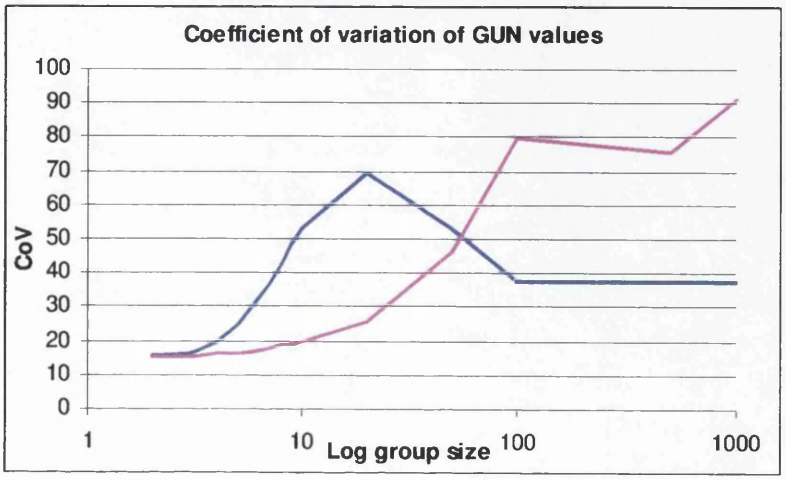
(a)



(b)



(c)



CHAPTER 5

PUBLIC INFORMATION USE AND LIMITED ATTENTION: A COST TO INFORMATION GATHERING

ABSTRACT

Public information theory suggests that animals sharing information concerning the availability of food resources may experience benefits to long-term intake rates, compared with foragers that do not. In an unpredictable environment, where food patches may contain variable amounts of prey, foragers sharing information relating to their prey capture success will be able to generate more accurate and up-to-date estimates of patch quality, than individuals relying purely on their own foraging success. Sharing information also ensures that each forager holds the same estimation, reducing conflict over when to quit a patch in tightly cohesive groups. However, this theory relies on the assumption that animals may acquire information without paying a cost. Research has shown that animals dividing their attention between two or more tasks, suffer a decreased performance at each task. I present a model here with which I examine the foraging success of group animals, when individuals must divide their attention between two tasks: personal foraging, and scouting for information signals. As more attention is directed towards scouting, a cost is incurred by an animal as a reduced success at personal foraging.

Using results from previous chapters I predict the cost at which information sharing is no longer beneficial, above non information sharing groups. I demonstrate here that these cost values are in fact higher than those predicted – foragers are required to pay a higher cost than envisaged before there is no longer a benefit to information sharing. There is thus a point at which foragers are reaping a benefit from public information, but not paying a cost to personal foraging. Increasing the cost to personal foraging only increases the length of time spent within a patch, whereas public information effects the *total* time spent foraging. The relative use of public information is therefore dependent upon the travel time between patches. I present a formula that can be used to calculate the relative benefit of information sharing, for a given set of parameter values.

INTRODUCTION

The work carried out so far in this thesis, and in previously published studies (e.g. Clark and Mangel 1984, 1986; Valone, 1993; Ruxton, 1995b) demonstrates that animals in a foraging group can use the prey capture information of other foragers, in order to make improved estimates of the decreasing quality of depleting food patches. But this work ultimately depends on the assumption that this public information is cost free, so that animals are able to acquire information made available by other foragers pertaining to their prey capture success, without any loss to themselves in terms of personal foraging. However, this is an unrealistic scenario, since animals will often face constraints in the acquisition of public information due to limits in their sensory attention and neural processing power (Templeton and Giraldeau, 1995b; Desimone and Duncan, 1995; Lima and Bednekoff, 1999; Dukas and Kamil, 2000; Dukas, 2002; Dukas and Ellner, 2003; Clark and Dukas, 2003). In particular, they are likely to be limited in their ability to detect public information signals when they are involved in personal foraging. Lima and Bednekoff (1999) showed that while dark-eyed juncos (*Junco hyemalis*) were able to detect approaching predators whilst they were feeding, their ability to do so significantly reduced compared to when their head was raised. In order to maximise anti-predatory vigilance the birds had to raise their heads, at the expense of feeding.

In a previous model (Chapters 3 and 4) we demonstrated that in a patchily distributed and depleting environment, sharing public information of prey capture events offers benefits to foragers in cohesive groups over groups not sharing public information, when there is no cost to information acquisition. When feeding in an unpredictable environment, foragers sharing public information made better estimates of the decreasing patch quality and were able to quit each patch closer to the optimal threshold level, than groups not sharing such information but basing their estimate of patch quality purely upon their own foraging success. This was the case regardless of group size. Information sharers experienced low variance in capture rates as a result of this, because they were able to allocate foraging time more efficiently, spending time in the more profitable patches and less time in the less profitable patches.

Groups not sharing public information were less able to generate accurate estimates of patch quality and were less able to allocate patch time efficiently, often over- or under-utilising patches to a great extent.

Here, we develop this model further to examine the extent to which public information use remains beneficial to cohesive foraging groups when there is a cost to its acquisition, in terms of reduced personal foraging success through limited sensory attention.

MODEL DESCRIPTION

Prey environment

We simulated an environment in which prey resources are distributed unevenly between a series of 500 discrete patches, with the number of prey on any patch being drawn from a negative binomial distribution with parameters $\alpha = 31.25$ and $\lambda = 8$. The number of prey in each patch was generated using the random number rejection technique, (following Evans et al, 1993a) where α defines the probability of finding prey, and λ defines the number of attempts in which prey is not found until the x^{th} success. There are thus a mean number of 250 prey items per food patch, with a variance of 8062.5. Previous simulations have shown that in such a highly variable environment there is a clear benefit to sharing public information in tightly cohesive foraging groups (see Chapters 3 and 4, but also Valone, 1993; Ruxton, 1995b).

Patch quitting

In order to maximise long-term capture rates, foragers aim to quit each food patch when its prey resources have been harvested down to a threshold level. Using a modified version of a formula developed by Iwasa et al (1981) we model how foragers in cohesive groups may estimate the decreasing quality of a food patch, under two circumstances: public information sharing and non-information sharing.

Foragers in groups sharing public information maintain estimates of patch quality which are equal to all other foragers in the group, since all foragers have the same information of patch quality. Thus, the group estimates when to leave a patch at exactly the same time. Foragers not sharing public information will generate patch estimates based solely upon their own foraging success. One way in which they can do this is to assume that each other forager in the group experiences exactly the same foraging success as itself (group foraging model - Chapter 3). However, as group size increases this assumption becomes more and more unrealistic (Chapter 3). We therefore also examine a second version of the group foraging estimator, designed to remove the bias in patch estimation seen in very large groups (group size-biased model - Chapter 4).

Regardless of the estimator used, individuals in non-information sharing groups will still likely have different estimates of patch quality to other foragers in the group, and will therefore want to quit patches at a different time. In order to maintain group cohesiveness, groups employ one of three patch-quitting strategies to decide when to quit patches:

1) First - the group leaves with the first individual whose estimate, E, falls below C.
2) Leader - the group leave when the E of one particular individual, for example the most dominant member of the group, falls below C.
3) Paired - the group leave when the estimate of any two individuals falls below C.

We examine the foraging efficiency of groups using each of these non-information sharing patch-quitting strategies, using both versions of the estimator model, and compare these to groups sharing full public information. In each simulation we examine these in groups containing 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 20, 50, 100, 500 and 1000 individuals, visiting a series of 500 food patches. We then compare these to simulations run here, also visiting a series of 500 food patches, with groups sharing public information with a cost to information acquisition (Totalinfo-with-cost). Each simulation was repeated 2000 times.

Cost of information acquisition

Using a modified version of a previous model (Chapter 3) we assume that a cost is incurred by foragers dividing their attention between two activities: personal foraging, and 'scouting' for the prey capture signals of other foragers. Although these two activities are not mutually exclusive, scouting impairs the foraging ability of an individual due to the limits of its sensory attention, and so the cost of scouting is introduced as a reduced likelihood of finding prey during foraging. Studies show that while they are not mutually exclusive, focusing on a foraging task can impair vigilance (Lima and Bednekoff, 1999; Dukas and Kamil, 2000; Guillemain et al, 2001). A higher cost means that on any search attempt a forager is less likely to find prey, because they are less likely to notice a prey item themselves, if they are busy observing the foraging activity of others.

We incorporate the cost of scouting into this model as a probability function to the foraging success of an individual, reducing its sensory attention span. On any search attempt the likelihood of a forager finding a prey item is a decreasing function of the number of prey remaining in a patch – as the number of prey in a patch decrease it becomes harder to find one. With the incorporated probability function, whenever a prey item is discovered, the forager still stands a chance of not 'noticing' the prey depending upon the associated cost value. The higher the cost to information acquisition, the lower the 'finding' value incorporated into the probability function.

Each time a forager encounters a prey item on a search attempt, the function generates a random number between 0 and 1. If this number is higher than the 'finding' cost value, the forager does not find prey on that particular search attempt – it fails to notice it, despite making a correct discovery. For example when a forager is devoting 100% attention to scouting, its foraging ability (and thus its finding value) is 0 because all its attention is directed elsewhere. So it will never notice prey, regardless of how often it makes successful search attempts, and will thus suffer a foraging success of 0. Conversely, when public information acquisition is free there is no conflict between foraging and scouting, and the finding value will be 1, so providing the initial search attempt was successful the forager will always notice

prey. This cost function does not affect foragers when no prey is present but only when prey is available to be discovered on a given search attempt.

Modelling the cost to public information use in this way mimics the way in which limited sensory attention is likely to affect foragers in the wild. Simply subtracting a given percentage from the total number of prey found at the end of foraging, to simulate a reduction in foraging efficiency, would be neither realistic nor accurate. Limited attention would most likely influence the time spent searching for a given number of prey, rather than the number of prey actually found, thus affecting prey capture rates in a different way. This can be demonstrated using simple calculations. For example if a forager finds 100 prey in 100 time units, subtracting 20 prey to simulate an information acquisition cost of 20% would reduce its prey capture rate from a value of 1 to a value of 0.8. Capture rate is calculated by dividing the number of prey found by the time spent foraging, so when a forager finds 100 prey in 100 time units the capture rate = 100/100 = 1. Subtracting 20 prey items from this value, to mimic a cost of 20% means that the forager has only found 80 prey, and thus the capture rate = 80/100 = 0.8.

More realistically, a forager with limitations to its sensory attention will spend on average 20% longer searching for those 100 prey items because it will sometimes not detect prey, and will thus spend longer searching for the same number of prey. In this case, the number of prey remains at 100, but the time to find this number of prey will increase to 120 units. The capture rate will therefore be 100/120 = 0.83. Using this method, we repeated each simulation with the Totalinfo-with-cost strategy, increasing the cost value in increments of 0.01, (i.e. increments of 1%) until each group experienced individual capture rates equal to those of each of the non-information sharing strategies, obtained during previous simulations (see Chapters 3 and 4). This was repeated for groups of each size listed above.

RESULTS

Cost values to information acquisition

Figures 5.1 and 5.2 display the cost values associated with public information acquisition. Figure 1 shows the benefit seen by Totalinfo groups over each of the other three non-information sharing patch-quitting strategies (First, Leader and Paired), obtained during previous simulations using the models presented in Chapters 3 and 4. This benefit is calculated in terms of the reduction in capture rate experienced by each strategy, compared to Totalinfo. For example, a group of 100 individuals using the First strategy experiences a capture rate that is 95.4% of that experienced of Totalinfo. Figure 5.2 shows the predicted cost value obtained from these percentage values, and is simply the percentage value in Figure 5.1 subtracted from 100, (the difference between Totalinfo – strategy) to give the cost value used in the probability function. As the percentage decreases the relative benefit seen by Totalinfo increases - in this example the cost value is 4.6%. This gives the value we should predict that needs to be incurred by Totalinfo groups before there is no longer any benefit to sharing public information. We call this the calculated cost. Shown on the same graphs are the actual cost values obtained during the repeated simulations performed here, at which the capture rates of Totalinfo-with-cost groups equalled those seen by the non-information strategies. We call this the numerical cost.

As described in previous chapters, the benefit to groups sharing public information is greatest when group size is large (Figure 5.1). Small groups see little or no increase in prey capture rates, but in larger groups sizes there is greater benefit to sharing public information. Figure 5.1 shows that the benefit experienced by Totalinfo groups, without any cost to information acquisition, remains close to 0 in groups up to 20 individuals. But in larger groups this benefit increases over non-information sharing groups due to their inefficiency as patch quitters (see Chapters 3 and 4 for a full discussion). The cost of this may be quite considerable in the largest groups.

Using the original group foraging estimator model, both First and Paired groups suffer up to a 10% decrease in capture rates, compared to Totalinfo groups. The

Leader strategy suffers to an even greater extent, seeing more than a 25% decrease in prey capture rates in groups of 500 individuals. Using the group size-biased model, non-information sharing strategies fare even worse. All three strategies experience up to a 55% decrease in prey capture rates in the largest groups, compared to Totalinfo groups, where group size is greater than 20 individuals.

The numerical cost values, obtained during the simulations performed here, are in good agreement with these findings. The actual cost incurred by Totalinfo-with-cost groups, in order to equalise prey capture rates with each of the other three patch-quitting strategies in previous simulations, remains similar to, but consistently lower than the calculated cost values in all cases (Figure 5.1). That these numerical costs are consistently lower is interesting, because it suggests that the percentage loss seen by First, Leader and Paired strategies compared with Totalinfo groups is different, albeit only slightly, from the cost required to produce the same capture rates in Totalinfo-with-cost groups. For example, in Figure 5.1a, a group of 100 individuals using First strategy achieves only 95.4% the capture rate of the Totalinfo strategy. We would therefore predict that a 4.6% cost would need to be incurred by Totalinfo in order to equal its capture rate with that of the First strategy (seen in Figure 5.2). But in fact, these simulations show that this is not true. Instead, simulations here show that Totalinfo-with-cost groups should be reduced to 94% efficiency, with a cost of 6% to information acquisition, in order to decrease the capture rate to that of the First strategy. Hence, groups sharing public information should in reality pay a higher cost to remove the benefits of public information use than predicted from relative benefits alone.

This disparity between calculated and numerical cost is likely to be a result of the travel cost incurred by foragers between patches. Prey capture rates are calculated over the total time spent foraging, which is the time spent in patches plus the inter-patch travel time, but the cost value to information acquisition only affects the time spent foraging in patches. The inter-patch travel time remains constant regardless of this and so the total time spent foraging does not increase in direct proportion to the cost involved.

Foraging efficiency when public information is costly

Group foraging model - Figure 5.3 shows the capture rates obtained from previous simulations, of foraging groups sharing public information with no cost (Totalinfo), compared with each of the non-information sharing patch-quitting strategies (see Chapter 3 and 4). Also shown are the prey capture rates of groups sharing public information with a cost to information acquisition (Totalinfo-with-cost). The cost incurred by Totalinfo-with-cost groups is the calculated cost, displayed in Figure 5.2. As described previously (Chapters 4 and 5) the prey capture rates of Totalinfo remain constant, at a value of approximately 0.205, for all group sizes. Results from the original group foraging model (Figure 5.3a, b, c; also see Chapter 4) shows that the First strategy experiences a decline in capture rate as group size increases. Capture rates fall to 0.18 in groups of 50 individuals, rising again to between 0.19 and 0.195 in the largest groups of 100, 500 and 1000 individuals (Figure 3a).

Totalinfo-with-cost groups see a fall in capture rates, as we would expect because of the cost factor, but these values remain higher than those seen by the First strategy. Thus, the predicted cost value that is required to decrease capture rates of Totalinfo groups to that of the First strategy, does not do so. Rather, the capture rates of Totalinfo-with-cost fall to a value of about 0.193 in groups of 20 and 50, and then rise again to between 0.195 and 0.2 in the larger groups, and are consistently higher than the First strategy. A very similar pattern occurs for the Paired strategy (Figure 5.3c). As group size increases, the capture rate of the Paired strategy decreases from 0.205, to a value of 0.1082 in groups of 50. In larger groups, the capture rate increases again to between 0.195 and 0.198. As with the First strategy, Totalinfo-with-cost sees prey capture rates consistently higher than the Paired strategy, even though the cost incurred is predicted to lead to these being equal. Rather, capture rates fall with increasing group size to a value of 0.19 in groups of 50 individuals, and then increases again in larger groups, to a value of about 0.2.

Prey capture rates for the Leader strategy also decrease with group size, but much more severely than both the First and Paired strategies (Figure 3b). In groups up to 20 individuals the decline is similar to First and Paired, lying between 0.19 and 0.2. But in larger groups the capture rate falls much more quickly, down to a value of

0.147 for groups of 500 individuals. There is a slight increase again for groups of 1000 individuals. The capture rates of Totalinfo-with-cost follow a similar decline, but again are always higher than those of the Leader strategy. At its lowest, the capture rate falls to 0.16 (groups of 500), but then rises again to 0.17 in groups of 1000 individuals. The reason for this discrepancy, as already explained, is probably due to the cost value being applied only to the time spent foraging in a patch, and not to the inter-patch travel time.

Group size-biased model - The results obtained using the group size corrected estimator model (Chapter 4; Figure 4d, e, f) show that, again, the three non-information sharing strategies suffer quite considerably compared to Totalinfo groups. In smaller groups capture rates remain constant, at a value of approximately 0.2, but in groups over 20 individuals in size all three strategies see prey capture rates decline dramatically with increasing group size (for a full discussion see Chapter 4), to a value of around 0.1. As with the original group foraging estimator, Totalinfo-with-cost groups experience capture rates that are slightly, but consistently higher than each of the non-information strategies.

Willingness to use public information when it is costly

The results shown in Figure 5.4 demonstrate to what extent the use of public information remains beneficial to foragers, when there is a cost to information acquisition. The graphs in Figure 5.4 show the difference between the predicted cost values (calculated costs) and the actual cost values (numerical costs), required to reduce the capture rates of Totalinfo groups to those of the other patch-quitting strategies. This value shows the extent to which foragers should be willing to pay a cost, in terms of reduced personal foraging success, for public information made available by other foragers. When the calculated and numerical costs are equal, any benefit to information sharing is balanced by the cost incurred by foragers, and so public information use is not valuable (although it is not detrimental either). It is therefore not worth paying any cost for information acquisition, because there is no benefit over that if a forager were to simply concentrate 100% on personal foraging. As the numerical cost increases, foragers must pay a higher cost to information

sharing before their capture rates are as low as foragers not sharing public information. Thus the higher the numerical cost is in relation to the calculated cost, the more foragers should be willing to pay for public information, because the information is relatively more valuable.

So for example, if groups using the Paired strategy see a decrease of 13% in capture rate, in comparison to Totalinfo groups, then we would predict that Totalinfo groups should suffer a cost of 13% before their capture rates are level with this (this is the predicted 'calculated cost'). During these simulations, however, we may find that a cost of this value does not reduce the capture rates of Totalinfo groups to that of the Paired strategy, and that a higher cost value is required to do this – 19% (this is the numerical cost). The difference between calculated and numerical cost is thus 6%, and groups sharing public information must pay a cost 6% higher than that predicted, before the benefit of public information use is lost. If public information costs 15 %, it does not matter, because foragers still see a benefit over non-information sharers. The foragers should be willing to pay anywhere up to a 19% cost, for using public information. The greater the difference between calculated and numerical cost, the more willing foragers should be to use public information.

Group foraging model -The results in Figure 5.4 show that the benefit to public information use increases with group size. In groups which contain fewer than 8 individuals, there is little difference between calculated and numerical costs. Compared with the First strategy information sharers see a 2% benefit in capture rates over non-information sharers, but also pay approximately a 2% cost before capture rates fall to those of the non-information sharers, so there is no real benefit to sharing public information. The cost cancels out the benefit. In larger groups however, the difference is greater. Groups of 20, 50, 10, 500 and 1000 see a difference between 2 and 8%. Information sharers in these groups must pay a higher cost than the benefits incurred due to information sharing, before their capture rates fall to that of the First strategy. They see a benefit to public information use over and above the cost they pay for its acquisition. This is similar for groups using the Leader strategy, although in larger groups, the difference is higher: between a value of 6 and 8%. Compared with the Paired strategy, the difference between calculated cost and numerical cost is similar to the First and Leader in smaller groups. The difference is also very close to

0 in very large groups. But in groups containing 10 and 20 individuals the difference is very high, reaching a value of 13% for groups of 10, and 9% in groups of 20. In other words, groups sharing public information should be willing to pay the highest cost (up to 13% higher than predicted) in groups of 10 or 20 individuals, compared with the Paired strategy. On the other hand, when group size is larger, or smaller than this, they should be less willing to pay a cost than with either of the other strategies.

Group size-biased model – Results using the group size-biased model are similar to those in the original group foraging model. In small groups, the difference between calculated and numerical costs are small, and hence any costs to public information use balances out the benefits. Similarly, in very large groups (500 and 1000 individuals) differences are low, for all strategies except the Leader. Compared with Leader groups, the difference remains between 2 and 7% in large groups. In small and intermediate sized groups (10, 20, 50 and 100 individuals) the difference increases to between 2 and 8%. This occurs for all three strategies, but also occurs in large groups for the Leader strategy. This again indicates that foragers should be willing to pay a higher cost to information acquisition when in groups of between 10 and 100 individuals, than in smaller of larger groups, because the rewards they get in return will be higher than the cost incurred.

PREDICTING THE VALUE OF INFORMATION USE

We can in fact predict the numerical cost to public information use for groups using the Totalinfo strategy, from the calculated cost, providing we know the average length of time spent in a patch by the Totalinfo group (F_T) and a non-information sharing group (F_F), and the average inter-patch travel time suffered by each individual (T). Where F_T is always 100% and F_F is a proportion of this value, the difference between the two represents the calculated cost, μ; for instance if F_F is only 90% of F_T then the difference is 10, and the cost value is $\mu = 0.1$. Thus $F_F = F_T - \mu$, or $F_T(1-\mu)$.

However this calculated cost function ignores the time spent by each forager travelling between patches, T. The total time spent foraging for Totalinfo groups is $F_T + T$, and for non-information sharing groups is $F_F + T$ and so

$$1-\mu = \frac{F_T + T}{F_F + T}. \tag{1}$$

The numerical cost value obtained in the simulations performed here is denoted by δ. From equation (1) we can see that

$$1-\delta = \frac{F_T}{F_F} = \frac{F}{F_F}$$

$$\Rightarrow F_F = \frac{F}{1-\delta}, \tag{2}$$

and so

$$1-\mu = \frac{F+T}{\left(F/1-\delta\right)+T}$$

$$\Rightarrow \frac{(1-\mu)F + (1-\mu)T}{1-\delta} = F+T$$

$$\Rightarrow \frac{(1-\mu)F}{1-\delta} = F + \mu T$$

$$\Rightarrow 1-\delta = \frac{(1-\mu)F}{F+\mu T}. \tag{3}$$

We can also rearrange equation (1) to show that

$$\mu = \frac{\left(F/1-\delta\right)+T-F-T}{\left(F/1-\delta+T\right)}$$

$$= \frac{F\left(1/1-\delta-1\right)}{\left(1/1-\delta+T\right)}$$

$$= \frac{F\delta}{(1-\delta)F+T}. \tag{4}$$

Thus, the calculated cost, μ, can be written as shown in equation (4).

By rearranging equation (4) we can find a similar formula that will allow us to predict the numerical cost, taking into account the inconsistency caused by inter-patch travel time.

Since $\frac{(1-\delta)T+F}{(1-\delta)T+F}=1$,

equation (1) can be re-written as:

$$\Rightarrow 1-\mu=\frac{(1-\delta)T+F}{(1-\delta)T+F}-\frac{F\delta}{(1-\delta)T+F}$$

$$=\frac{(1-\delta)F+(1-\delta)T}{(1-\delta)T+F}=\frac{(1-\delta)(T+F)}{(1-\delta)T+F}$$

$$\Rightarrow((1-\delta)T+F)(1-\mu)=(1-\delta)(T+F)$$

$$\Rightarrow F(1-\mu)=(1-\delta)(T+F)-(1-\delta)T(1-\mu)$$

$$=\mathrm{F}(1-\mu)=(1-\delta)(T+F-(1-\mu)T)$$

$$\Rightarrow 1-\delta=\frac{(1-\mu)F}{T+F-(1-\mu)T}. \qquad (5)$$

Thus, providing we know the parameters of the environment in which an animal is foraging, and we have data of the prey capture rates experienced by groups both sharing and not sharing information, we can calculate accurately the value of the information to such foragers.

DISCUSSION

The results presented here indicate that there is an inconsistency between the cost values which are predicted to reduce the prey capture rates of groups sharing public information to those of the other patch-quitting strategies (calculated costs), and the cost values which actually do so (numerical costs). These simulations show that numerical costs are consistently higher than those predicted. We present formulae which can be used to predict both calculate costs, and numerical costs, and the data from simulations show that both of the formulae are accurate. Foragers sharing public information must often pay a higher cost than predicted, before their capture rates decline to those of the non-information sharing strategies. As already mentioned, this inconsistency is likely to be due to the cost incurred by foragers travelling in-between food patches. Our model assumes that foragers pay a constant inter-patch travel cost of 400/N time units between every patch visit (where N = the number of foragers in the group). The capture rates for each strategy in the previous results are calculated over total foraging time, including this travel cost. Foragers pay a cost to information acquisition, which ultimately results in a longer time spent foraging for food in a patch. But the travel time between patches remains unaffected by this, so the total time spent foraging does not increase in direct proportion to the cost of information acquisition. Using the formula presented in equation (2) we can accurately predict the cost that foragers will be willing to pay, for the use of public information.

This travel-time effect is enough to explain the discrepancy between calculated and numerical costs seen in the results above. The smaller the inter-patch travel time, the more significant the cost factor becomes. This is important, because the difference between these two values, and the difference between the respective capture rates, allows us to visualise how profitable public information use might be in a group of foraging animals. As inter-patch travel time increases the capture rates of Totalinfo-with-cost groups will depart further and further from those of the patch-quitting strategy for a given cost value, and the use of public information becomes more and more valuable. With a very large travel time, the cost will become effectively

insignificant in relation and the foragers will see huge benefits to public information use in relation to the cost incurred for its acquisition.

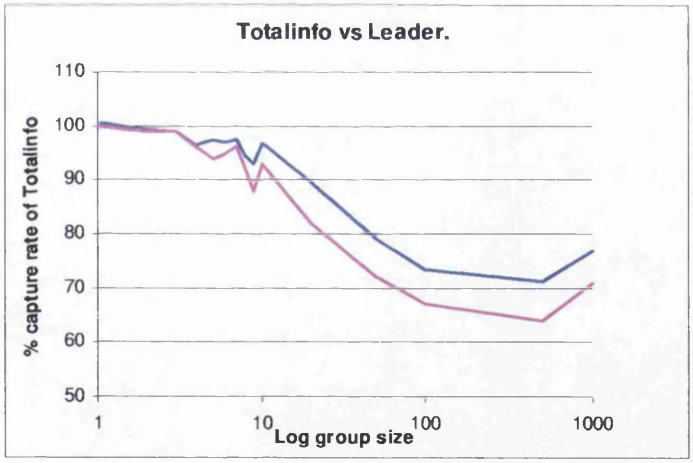
It seems intuitive then, that in the other extreme, when there is no travel time between patches, the cost factor will be at its true value, predicted by the calculated cost, and groups sharing public information will experience capture rates in direct proportion to the benefit observed over non-information sharing groups - i.e. calculated and numerical costs will be equal. However, this is in fact not the case. If we remove inter-patch travel time, the environment effectively becomes a single patch of infinite size, and groups do not ever leave - prey capture rates remain constant regardless of group size, or the patch-quitting strategy adopted by the group.

What this inconsistency between calculated and numerical cost values indicates, is that the use of public information tends only to be of any real benefit (when a cost is involved) to foragers in large groups, and when the cost of travelling between patches is high, thus supporting previous work (see Chapter 3). The difference between the calculated and numerical cost values reveals how valuable the use of public information is to foragers, and to what extent they should be willing to pay for its acquisition, in terms of reduced personal food discovery rate. In our simulations, groups consisting of less than 20 individuals see little, or no benefit to sharing public information over that of non-information sharing groups. In such groups any benefit to public information use is not worth paying for because any improvement in patch estimation is cancelled by a loss to immediate personal foraging success. Only when group size increases above this do foragers see there any real benefit to information use. In these groups the calculated and numerical cost do not match, because of the travel-time effect, and foragers see a profit above and beyond the cost they pay for information acquisition.

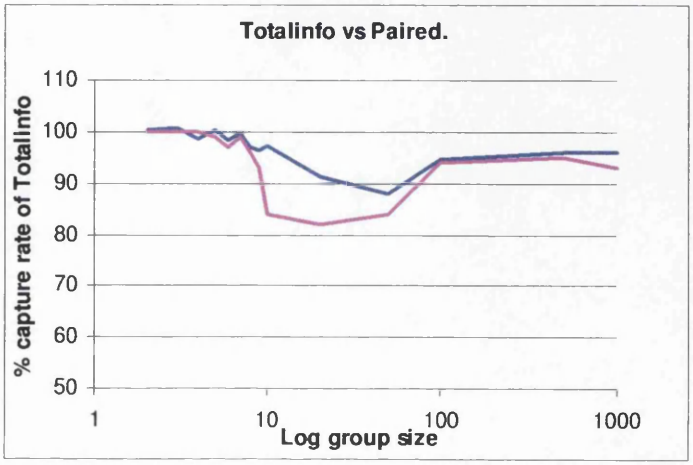
Figure 5.1 - Predicted and obtained cost values for information sharing. The % capture rate experienced by non-information strategies compared with Totalinfo implies the cost which should be incurred by Totalinfo before there is no longer any difference in capture rates (calculated cost, μ). The percentage loss in capture rate actually incurred by Totalinfo groups before this occurred (numerical cost, δ). Numerical cost values obtained during using original group foraging estimator **(a)** First, **(b)** Leader, **(c)** Paired; and group size corrected estimator **(d)** First, **(e)** Leader, **(f)** Paired. Calculated cost - blue, numerical cost - pink.

(a)

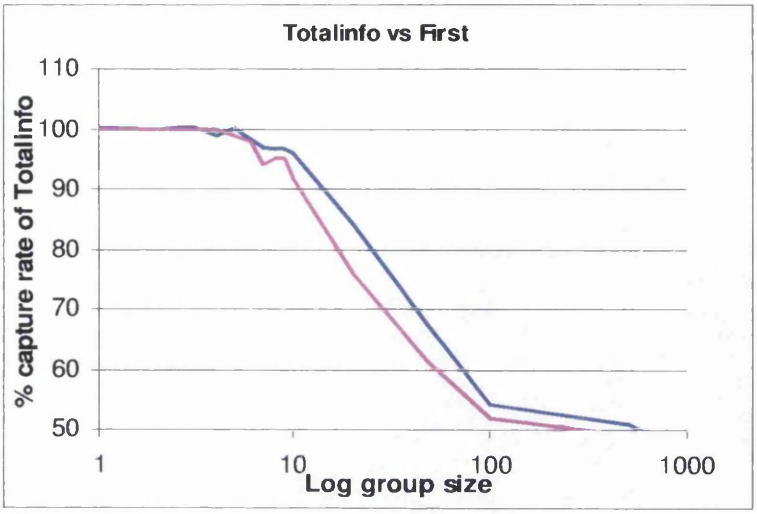
(b)



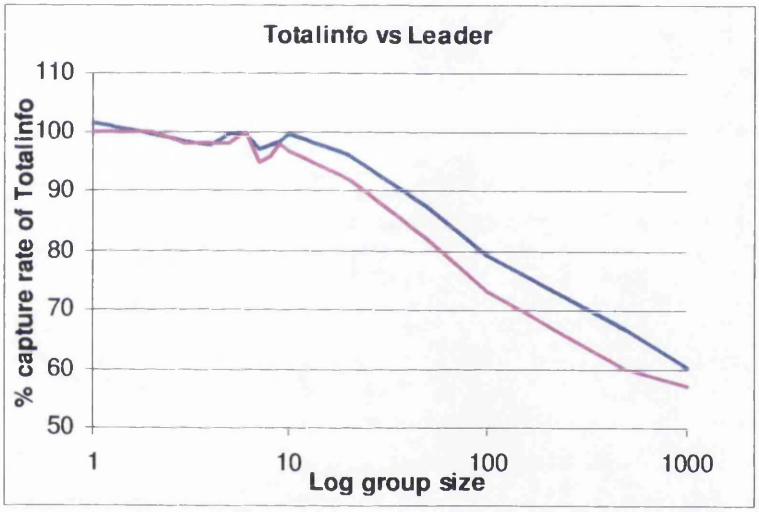
(c)



(d)


Totalinfo vs First
% capture rate of Totalinfo
110
100
90
80
70
60
50
1
10
100
1000
Log group size

(e)


Totalinfo vs Leader
% capture rate of Totalinfo
110
100
90
80
70
60
50
1
10
100
1000
Log group size

(f)

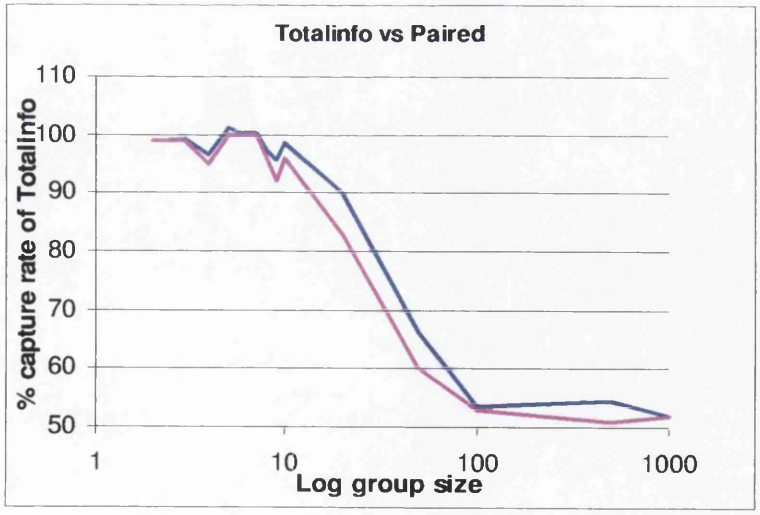
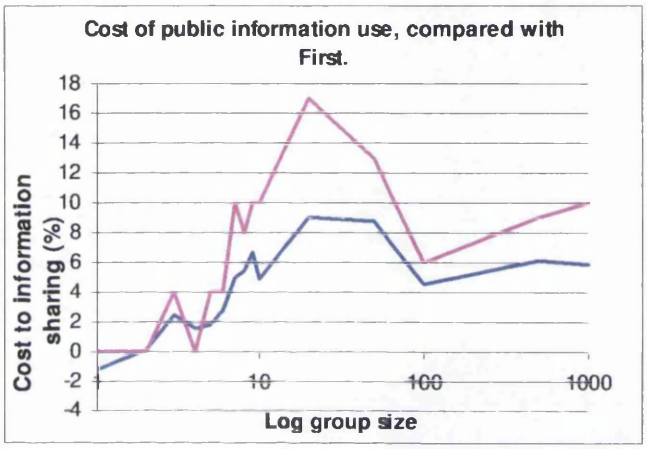
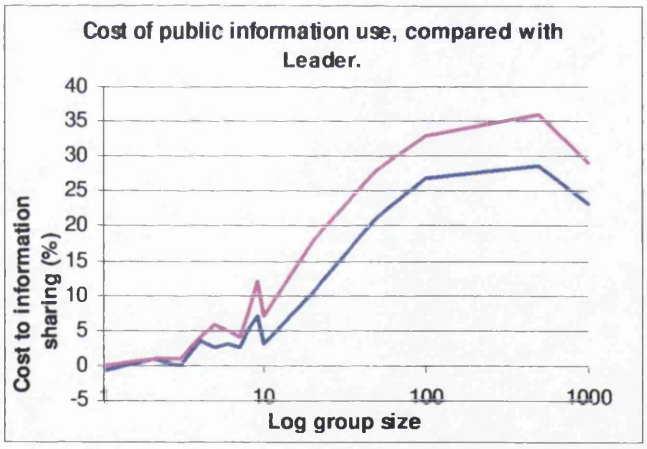

Totalinfo vs Paired
% capture rate of Totalinfo
110
100
90
80
70
60
50
1
10
100
1000
Log group size

Figure 5.2 – Cost to public information use. Calculated cost – the cost value required to equalise the capture rates of Totalinfo groups to those of First, Leader and Paired groups, predicted by previous simulations using original group foraging model: **(a)** First, **(b)** Leader, **(c)** Paired, and group size corrected estimator **(d)** First, **(e)** Leader, **(f)** Paired. This cost is obtained by subtracting the percentage benefit (shown in Figure 1) from 100. Numerical cost – the actual cost value required to equalise capture rates of Totalinfo-with-cost groups to those of First, Leader and Paired groups. Calcuated cost - blue, numerical cost - pink.

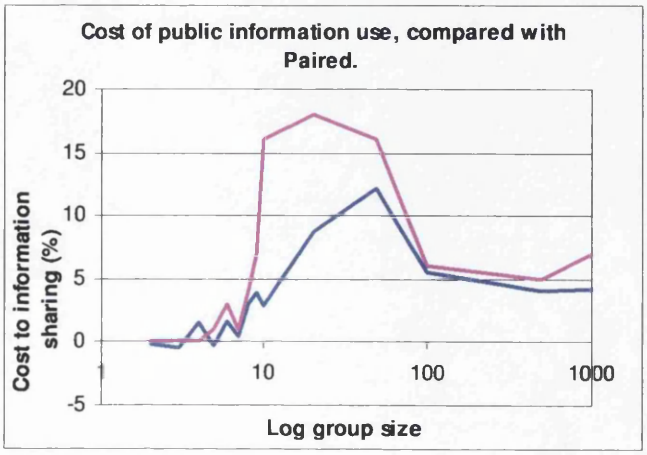
(a)



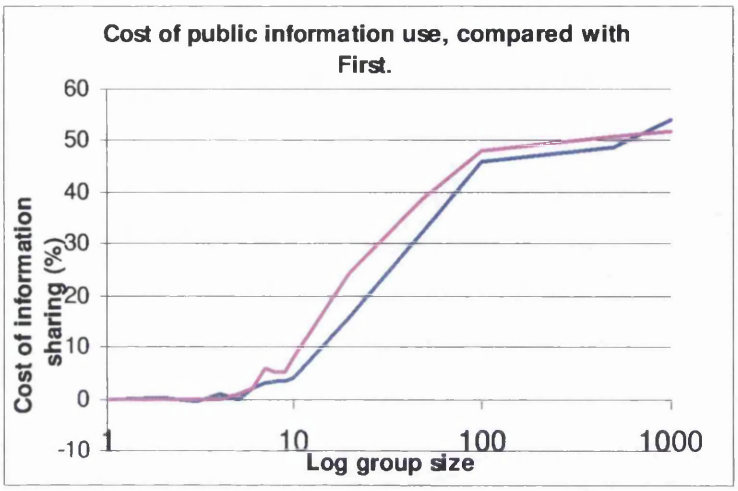
(b)



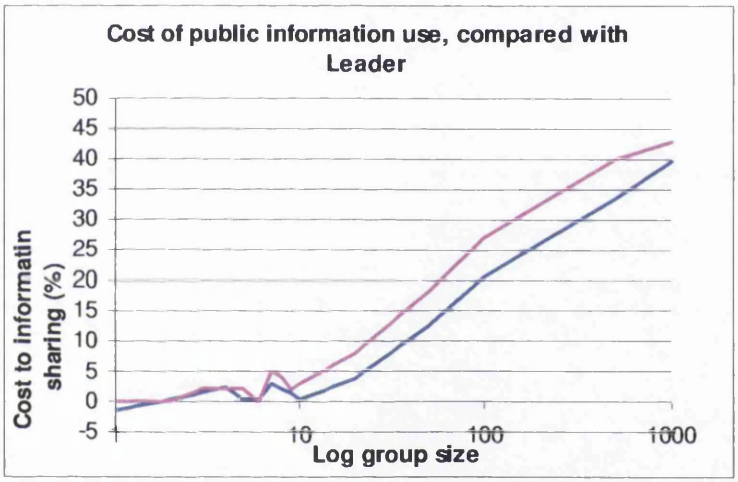
(c)



(d)


Cost of public information use, compared with First.
Cost of information sharing (%)
60
50
40
30
20
10
0
-10
1
10
100
1000
Log group size

(e)


Cost of public information use, compared with Leader
Cost to informatin sharing (%)
50
45
40
35
30
25
20
15
10
5
0
-5
10
100
1000
Log group size

(f)

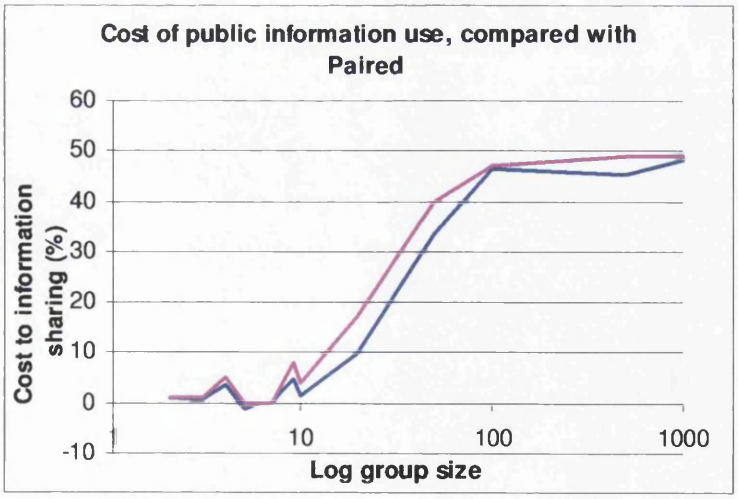
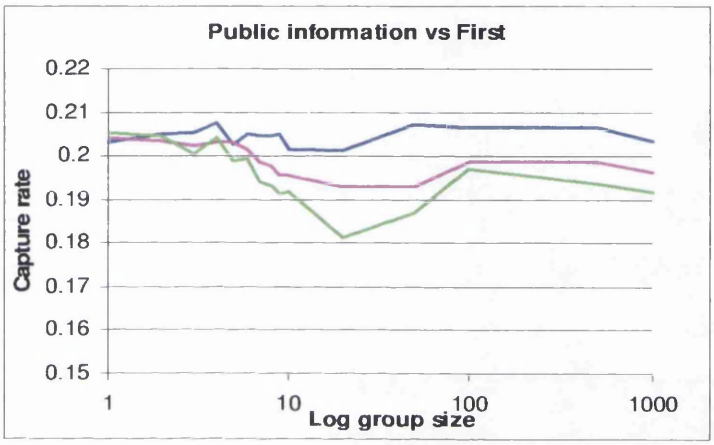
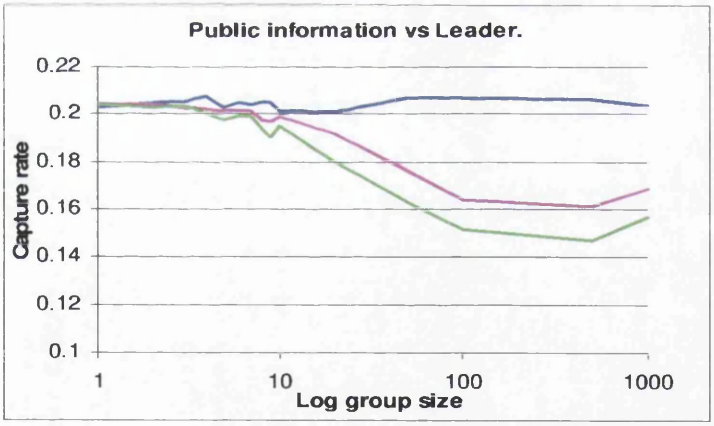

Cost of public information use, compared with Paired
Cost to information sharing (%)
60
50
40
30
20
10
0
-10
1
10
100
1000
Log group size

Figure 5.3 - Prey capture rates obtained by foraging groups sharing public information with no cost (Totalinfo), with an added cost to information acquisition (Totalinfo-with-cost), and each of the non-information patch-quitting strategies. Original group foraging estimator model: **(a)** First, **(b)** Leader, **(c)** Paired. Modified group size corrected estimator model: **(d)** First, **(e)** Leader and **(f)** Paired. The cost incurred by Totalinfo-with-cost groups is the calculated cost, predicted in previous simulations. Totalinfo - blue, Totalinfo-with-cost - pink, non-information strategy - green.

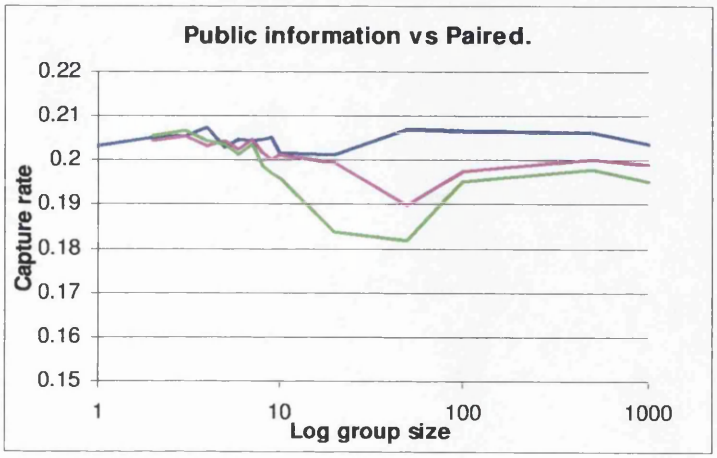
(a)



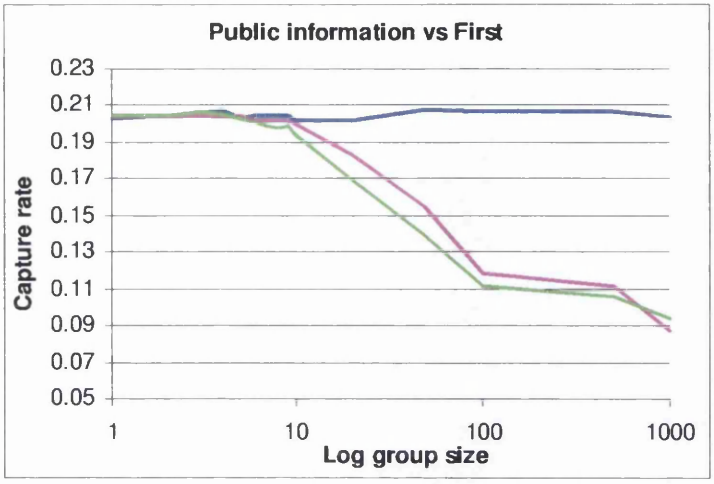
(b)



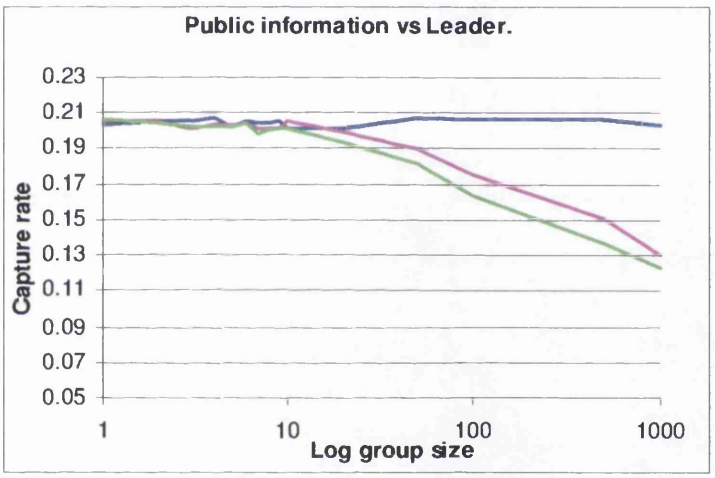
(c)



(d)


Public information vs First
Capture rate
0.23
0.21
0.19
0.17
0.15
0.13
0.11
0.09
0.07
0.05
1
10
100
1000
Log group size

(e)


Public information vs Leader.
Capture rate
0.23
0.21
0.19
0.17
0.15
0.13
0.11
0.09
0.07
0.05
1
10
100
1000
Log group size

(f)

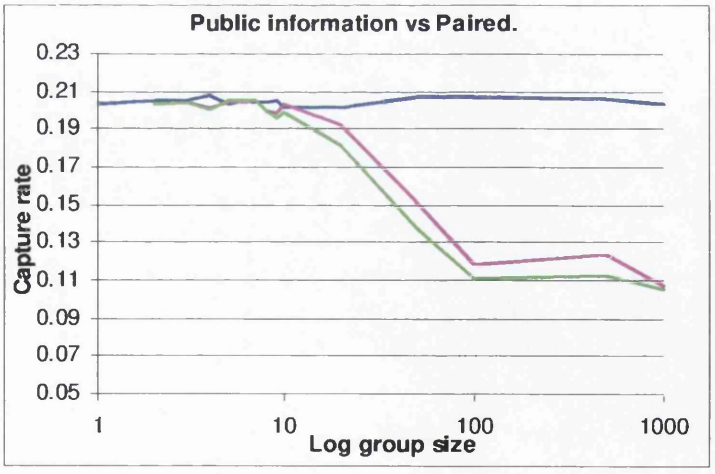
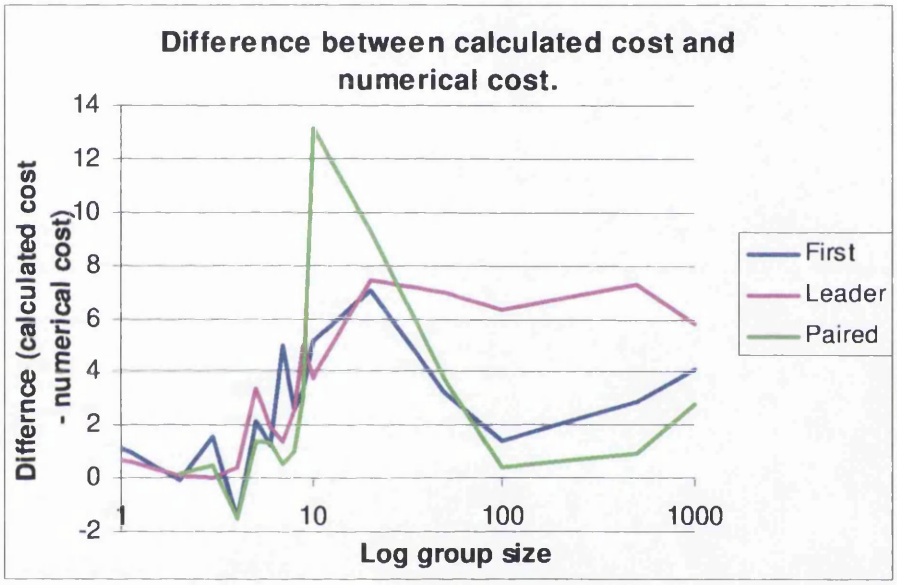
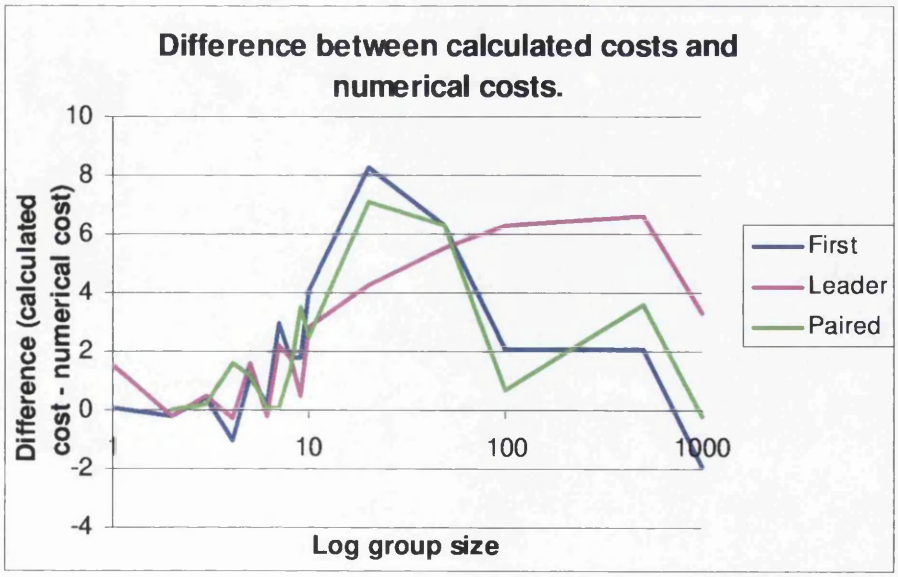

Public information vs Paired.
Capture rate
0.23
0.21
0.19
0.17
0.15
0.13
0.11
0.09
0.07
0.05
1
10
100
1000
Log group size

Figure 5.4 – Trading the cost and benefits of public information use. The difference between calculated cost – numerical cost shows to what extent public information use remains beneficial with a cost to information acquisition. The calculated cost is the cost predicted to reduce capture rates of Totalinfo groups to that of the non-information sharing strategies, directly derived from the observed benefits. The numerical cost is the actual cost incurred by Totalinfo-with-cost groups before capture rates were equal to those of the non-information sharing strategies. The greater the difference, the greater the benefit to foragers sharing public information. **(a)** original group foraging model, **(b)** group size corrected model.



(a)



(b)

CHAPTER 6

PARADISE LOST: THE VALUE OF PUBLIC INFORMATION USE WHEN INFORMATION IS UNRELIABLE

ABSTRACT

This thesis so far examines the effect of public information use on foraging efficiency by animals feeding in groups. Previous chapters examine the extent to which public information of successful prey capture events remains useful when there is a cost to its acquisition, but so far ignores the possibility that this information may be incomplete or inaccurate. In the natural world such information is rarely likely to be complete and totally accurate. Most animals are likely to receive only a fraction of the information available to them, and some of this information may be incorrect. In this chapter I develop a model to investigate the effect of public information use on the long-term efficiency of group foragers, when information is incomplete and erroneous.

I show that information infidelity is detrimental to the long-term foraging success of groups sharing public information. I demonstrate that the consequences of transmitting false prey capture signals (Mistakes) are far greater than missing true signals (Misses). Foragers missing signals underestimate the quality of a food patch, because they are not made aware of all prey capture events. They quit patches early because they expect the patch to be poorer than it really is: this increases sensitivity to poor patches, whilst in rich patches it makes little difference because prey is likely to be found soon after each Miss, except where they occur almost all the time.

Foragers receiving Mistakes also quit patches early. Since finding food suggests that they are in a rich patch, Mistakes lead foragers to over-estimate patch quality. The more food they find, the richer the patch must be. However, foragers are also aware of the prey distribution throughout the environment, and since food is being 'found' more frequently the patches must also be depleting more quickly. Foragers thus quit rich patches early, whilst remaining in poor patches too long.

INTRODUCTION

The animal brain is of only a limited size, and as such there is a finite level of work it can carry out at one time. Numerous studies have shown that animals are faced with constraints to information processing capacity. They have only a limited attention, and must divide their available cognitive resources between several tasks (Desimone and Duncan, 1995; Templeton and Giraldeau, 1995b, 1996; Vreven and Blough, 1998; Smith et al, 1999; Dukas and Kamil, 2000; Dukas, 2002; Clark and Dukas, 2003; Bergen et al, 2004; also see Eysenck and Keane, 1990). Animals should therefore allocate the most attention to the task of most importance.

However, dividing attentional resources in this way reduces the efficiency of each specific task. Vreven and Blough (1998) revealed that pigeons found it more difficult to detect recognised target objects when the number of non-target objects increased, and also when the number of target objects increased. Meanwhile, Dukas and Kamil (2000) demonstrated that blue jays were less able to recognise prey items in their peripheral vision when focussing on a difficult focal task, than when the focal task was easy.

In terms of foraging and information sharing, both of these studies suggest that animals are likely to suffer a decline in their ability to correctly recognise public information signals when searching for food. Animals paying a higher level of attention to personal foraging activity are more likely to make mistakes in their recognition of such signals, misinterpreting them as something else, or perhaps missing them entirely – this is particularly likely when foraging in large groups, where other foragers may interfere with the transmission of such signals by getting in the way, or by increasing background noise levels. Alternatively animals may misread innocuous signs or gestures as signals relating to prey capture events. Additionally to this Dukas and Clark (1995) note that vigilance cannot be sustained for long periods of time, and so we should expect that an animal will be more likely to make mistakes the longer it spends foraging.

In previous chapters I have shown that in an uncertain environment, where food resources are distributed patchily over a number of discrete and isolated patches (Chapter 3), animals feeding in cohesive groups may experience benefits over other groups in terms of long-term foraging success, if they share information about each successful prey capture event. By sharing public information each individual is able to maintain an accurate estimate of patch quality, and the group can allocate their foraging time more efficiently between profitable and non-profitable patches. Since all individuals also have access to exactly the same information they also have the same estimate of patch quality, and there is no conflict over when to leave patch a (see Chapter 3 for a full discussion).

I have further shown the extent to which public information remains beneficial when foragers must pay a cost for its acquisition, in terms of reduced personal foraging success due to limited sensory attention. At any one time a forager can either be involved in personal foraging or scouting for the prey capture information of others. Clearly, the more attention a forager pays to scouting, the less likely it is to find food itself. This work demonstrates that public information has the largest benefit when the cost of travelling between patches is highest (Chapter 5). Foragers scouting for public information will tend to spend more time in patches, because they are not finding prey as quickly as foragers devoting all their attention to searching, and so the total time spent foraging will be higher – but scouting does not affect travel time between patches, and so the total time spent foraging is lower than that predicted by its cost. The discrepancy between predicted and actual total foraging time indicates the true value of public information (see Chapter 5 for a full discussion).

Both of the studies mentioned above however, and (until recently) much of the literature examining information sharing, assume that information is accurate and completely reliable. Animals are assumed to make decisions and base their behaviour upon information that is exactly representative of their environment. The natural world is unlikely to be this simple, and often information may be incomplete or erroneous. As Giraldeau et al (2002) note, animals will often acquire information from other animals as a result of their decisions, (i.e. by watching their behaviour) rather than directly from the cues that led to this behaviour. Thus the information available is second-hand, biased to the perception, and the mental and physiological

state of the provider, and may already be inaccurate or misleading. In the extreme, this can lead to information cascades (Giraldeau et al, 2002) where individuals blindly copy each other and, for example, entire bird flocks may suddenly take to the air because one individual falsely perceives the presence of a predator. Clearly, if a predator is really present then this is likely to be beneficial. But if there is no predator, this behaviour is sub-optimal because it wastes metabolic energy and time that could be spent performing other activities, such as feeding.

In this chapter I describe a model developed to examine the long-term effects on foraging success for animals sharing public information, when this information is erroneous or incomplete.

MODEL DESCRIPTION

Prey environment

In keeping with previous models, I imagine an environment in which prey is distributed unevenly between a series of discrete and isolated food patches. The number of prey on any patch is drawn from a negative binomial distribution with parameters $\alpha = 31.25$ and $\lambda = 8$, using the random number rejection technique, (following Evans et al, 1993a) where α defines the probability of finding prey, and λ defines the number of attempts in which prey is not found until the x^{th} success. Each patch has a mean number of 250 prey items per food patch, with a variance of 8062.5. Previous work shows that public information use is at its most beneficial when patch variability is high (Chapter 3). Foragers have a knowledge of the prey distribution within the environment, but they do not know the number of prey available in each patch.

Erroneous public information

Upon entering a patch, foragers begin searching for food. At any given time one of two things can happen: a forager may find food or a forager may not find food. For

each prey capture that is made a signal is transmitted to all other foragers in the group. This informs them that a prey item has been found, and allows them to update their estimation of the prey availability in the patch. However we assume that this information may be inaccurate. Each time a signal is made, there is a chance that it will not received by the other individuals in the group. The signal may be lost through interference, or mistaken for something else. The probability of this occurring is defined by p. Each time a food item is found by a forager, the model generates a random number between 0 and 1. If this number is smaller than the probability factor p, the signal is considered lost, and will not be transmitted to any other foragers in the group. The number of prey in the patch still decreases by one, and the forager making the discovery acknowledges this, but the other individuals in the group do not. Note that p is a fixed probability, but can only happen when a food item has been found. This is called a Miss.

However, erroneous signals can also occur when food is not found. At any point in time there is a chance that a forager will transmit a prey capture signal (or something recognised as a prey capture signal) when no prey has been found. This occurs at rate Q and is dependent upon the number of foragers in the group, i.e. NQ per unit time. All foragers receive and recognise this false signal and adjust their estimates accordingly, but the number of prey remaining in the patch does not decrease. This is called a Mistake and can occur at any time that a food item has not been found. For simplification we never assume that some foragers receive this signal, while others do not. If a mistake signal is given it is observed by all foragers. I discuss how realistic this supposition is likely to be in the Discussion.

Patch estimation and quitting

In order to forage optimally, animals should remain feeding in each food patch until the available prey have been depleted to a certain threshold level, which is representative of the average overall expected capture rate for the environment (Charnov, 1976). We call this the optimal value of C – the optimal number of prey items remaining in the patch, or left-over-constant, LOC (Green, 1988). Using a modified version of a formula developed by Iwasa et al (1981) we model how foragers in cohesive groups may estimate the decreasing quality of a food patch

whilst sharing public information of all successful prey capture events. This estimator is written as

$$E(n,t) = \frac{\lambda + n}{\left(\exp\frac{NS_1 t}{P}\right)\left(\frac{\alpha+1}{\alpha}\right) - 1} \qquad (1)$$

where λ and α are parameters of the negative binomial distribution, N = the number of foragers in the group, S_1 = the search rate of one individual, t = the time spent in a patch at any given point, n = the total number of prey items found in a patch at time t, and P = the maximum size of the patch. As before we cannot denote a maximum patch size (i.e. the total space in which prey items can be found) when using a negative binomial distribution, because they have no theoretical upper limit. We must do this in order to calculate searching rates and prey capture rates however. Previous simulations show that with our selected values of λ and α we can be confident that no more than 1% of patches will contain more than 500 prey items. Additional simulations also show that replacing P = 5000 does not make any practical difference to optimal quitting values. In this study we can thus justify defining P = 500.

All foragers enter a patch at the same time, and remain there until they estimate that they have harvested the available prey resources down to the given value of optimal C. The ease with which prey resources are discovered depends upon their availability, so that as prey becomes scarce in the patch it will take relatively longer to find the next one. The time until the next prey discovery is calculated stochastically using an exponential distribution with a mean 1/R(X), where X is the number prey remaining in the patch. When a prey item is found it is allocated to a random forager within the group and X = X-1.

Foragers must estimate the number of prey remaining in a patch, depending upon how much time they have spent feeding in the patch, and how many prey items they have found in that time. Although all individuals in the group are sharing information of prey capture events, some of this information is erroneous – some capture signals are not transmitted to other foragers, while some signals refer to capture events that did not occur. Assuming that they know this, foragers must take this into account when

estimating prey depletion in the patch. The estimator for modelling this, shown in equation (1) therefore needs to be modified.

The parameter n no longer represents the number of prey items found, but the number *thought* to be found – i.e. the number of real food items found (d1) and the number of Mistakes (d2). Estimating the true value of X would be too complicated, considering the distribution of prey items within a patch, plus the number of observations made by all foragers in the group. I offer a simplified estimate which nevertheless provides a good approximation most of the time. The number of Mistakes, d2, has the expectation (N-1)Qt, and if we assume that foragers are aware of the likelihood of recording false signals, we can say that the expected number of true items found, X = n-NQt. We similarly assume that foragers know the likelihood of missing prey capture signals. However, this value X is only a fraction of the true number found. Depending on p, there are d3 items that have been missed, i.e. 1-(N-1)p/N. This method offers a simplified approximation of the expectation for X:

$$n - \frac{(N-1)Qt}{1-(N-1)p/N} \qquad (2)$$

We can simply substitute this into the estimator in replacement of n, so that we have

$$E(n,t) = \frac{\lambda + x}{\exp Rt\left(\frac{\alpha+1}{\alpha}\right) - 1} \qquad (3)$$

In previous simulations (Chapter 3) I demonstrated that sharing public information was beneficial because every individual shares the same estimate of patch quality, maintaining group cohesiveness and reducing conflict over when to quit a patch (Chapter 3). However, since foragers in this model no longer have the same information as everyone else, the group once again has a range of patch estimates. In order to try and conserve the cohesiveness of these groups and avoid conflict over patch departure decisions, foragers adopt the Leader strategy as described previously. This ensures that on average the group is not biased by runs-of-bad-luck (Valone 1993; Ruxton, 1995b; Chapter 3).

Finding the optimal values of C

Previous work has demonstrated the importance of finding the correct patch quitting values of optimal C (Chapter 3). Attempting to quit patches at a sub-optimal value of C can be detrimental because the foragers are trying to quit patches at a prey value that will not maximise long-term capture rates. As such, I must calculate the optimal value of C for each different scenario. I assume here that foragers are aware of the likelihood of receiving inaccurate information, and that they will alter their patch quitting behaviour to follow this. I calculate the optimal value of C for each combination of p and Q. I do this in the same way as with the previous model (Chapter 3). I simulate foraging activity over a series of 500 patches, forcing the foraging groups to quit patches at each possible value of C, recording the prey capture rate for each one and plotting the results. Each run of 500 patches was repeated 2000 times. The value of C yielding the highest capture rate (the peak of the curve) represents the optimal value of C. Figure 6.1 displays the optimal values of C obtained for a range of combinations of Q and p. Simulations show that there is no effect to optimal C for low values of p; Figure 6.1 therefore displays only results for p = 0.7 and above.

RESULTS - OPTIMAL C VALUES

We can immediately see from Figure 6.1 that as each of the error factors, Q and p, increase in value the optimal value of C decreases towards 0. As public information becomes less reliable in its content the foragers must remain in patches for relatively longer, depleting patches to a lower level before quitting, in order to optimise their long-term prey capture rates. When information is unreliable foragers are less able to estimate true patch quality, and they use their foraging time inefficiently, either because they remain too long in unprofitable patches or because they do not use profitable patches to their full potential. They must make up this cost by harvesting each patch more completely before quitting.

It was noted in Chapter 3 that foragers restricted in their patch quitting ability (due to the patch quitting strategy employed by the group) could maximise their foraging

success by aiming to quit patches when the remaining number of prey in a patch was very low. This is analogous to the prediction by the marginal value theorem (Charnov, 1976) which states that as the travel time between patches increases, foragers much harvest each patch to a lower level in order to make up this extra travel cost. In the case of the patch quitting strategies, the foragers much make up the cost of indecision in a patch and quitting patches too early. In the simulations run here, the cost is imposed by inaccurate information. Foragers must aim to quit patches at a low level in order to make up the cost of inaccurate patch estimation. The optimal value of C for groups sharing complete and perfectly accurate information will no longer be the most profitable for these foragers, because their information is not complete or perfectly accurate.

The rate of Mistakes, Q, has a much more significant effect on optimal values of C than the probability of Misses, p. Relatively small values of Q decrease optimal C considerably, whereas p has no observable effect at all until it is approaching 1. This indicates that gaining false information about capture events that never occurred is more important than missing information about prey capture events that did occur. Foragers updating their estimation of patch quality on the assumption that prey has been found are immediately assuming that there are more prey resources in the patch than there really are. Patches described by a negative binomial distribution tend to be either very rich or very poor, so finding prey indicates a rich patch – the more prey that is found, the richer the patch must be. Where this information is false, foragers conclude not only that the group as a whole is experiencing more successful foraging than is really true, but also that the patch is richer than it is. This encourages them to remain in the patch for longer. On the other hand, a forager's estimation of patch quality is constantly decreasing anyway, as a factor of the time spent in the patch. Missing a prey capture signal does not directly affect patch estimation – this simply continues to decrease as it would have done had no prey been found and the group continues foraging as normal. Since prey *has* been found the prey capture rate of the group actually increases, and they are more successful than they realise. When misses do not occur very often, this is not likely to affect the group significantly. When p is very large however, and almost all signals are lost the foragers are led to believe that even rich patches are very poor, encouraging them to quit patches early. In order to

make up this cost and forage optimally, they must harvest each patch down to a lower level before quitting.

It is interesting to note that in larger groups the optimal value of C increases, for both Misses and Mistakes. For foragers transmitting false signals the faster rate of patch depletion in large groups offsets the tendency to over-estimate the quality of the patch and remain there too long, expecting them to be rich. They deplete the patch quickly enough so that they leave before time has been wasted, and thus increase their overall rate of gain from the environment – meaning that they harvest each patch to a lesser extent before quitting, in line with the marginal value theorem (Charnov, 1976). This occurs for smaller groups where Q values are low, because the patches are not deemed to be as high value as when Q is large.

Foragers Missing signals also see a small incline in optimal C values with increasing group size. Missing signals is likely to encourage foragers to quit patches sooner than they would do ordinarily, because they believe it to be a lower value than it really is. In large groups this will be exaggerated because signals will be missed more frequently, and the group will want to remain foraging in a patch for a shorter time than smaller groups. In a rich patch, where food is readily present and prey discoveries are relatively frequent, this is not likely to affect patch quitting more than it does smaller with groups - the frequency of Misses will increase with group size; but only in line with the rate of prey discovery. In poor patches however, large groups will both discover prey more easily and Miss signals more frequently, but because the patch is already poor they are likely to be more sensitive to the quality of the patch. They will spend less time in unprofitable patches and inadvertently forage more efficiently, the consequence of which is to utilise each patch to a lesser extent.

Foragers with erroneous or incomplete information of prey capture events are less able to accurately estimate the true value of prey available to them in a patch. They are severely hampered in their ability to forage efficiently as they are not able to utilise a patch to its full potential. In order to make up this deficiency (in a similar way to foragers travelling long distances between patches) they must harvest each patch down to a low level of C. However, comparing the two directly is difficult because their relative values change over time. The effect of p decreases as the patch

runs out of prey, since there are fewer prey signals to Miss. Mistakes on the other hand remains constant regardless of the prey availability in a patch, and are only dependent upon the number of individuals foraging in the group.

Foraging efficiency with erroneous information

Using the optimal values of C obtained from the above simulations, I examine foraging and patch quitting behaviour using the same model, in the way described in the methods section. Groups sharing public information of all prey capture events forage over a series of 2000 patches, aiming to quit each patch at the pre-determined optimal value of C. I varied both the rate of Misses (p) and Mistakes (Q), while holding the other constant at 0. I vary Q through 0.01, 0.03, 0.05, 0.07 and 0.1; and p through 0.7, 0.8, 0.9, 0.95 and 1. Each simulation was carried out for groups containing 2, 3, 4, 5, 6, 7, 8, 9, 10, 20, 50, 100, 500 and 1000 individuals.

From each of these trials, we collected the long-term individual prey capture rate, the average time spent in each patch, the actual prey patch quitting values (the giving-up-number or GUN), and the coefficient of variation of GUN.

RESULTS - PATCH ESTIMATION

Prey capture rates – Figure 6.2 displays the prey capture rates obtained from the above simulations. For Misses, there is a general trend for capture rates to decrease, as p increases (Figure 6.2a). Although there is no clearly discernible trend with increasing Q, the capture rates for Mistakes (Figure 6.2b) are considerably lower for all values of Q than for both foragers sharing complete and accurate information (see previous work: Chapter 3) and also foragers with a high rate of Misses. Foragers sharing perfect public information experienced prey capture rates of about 0.205, for each group size examined. Suffering Mistakes immediately reduces this to between 0.12 and 0.14. In larger groups, consisting of 50 or more individuals, there is a rise in capture rates, but this is so slight as to be almost ineffectual. Groups suffering Misses barely experience any decrease in capture rates where p = 0.7 and 0.8, but for p = 0.9,

0.95 and 1 this drops to between 0.2 and 0.18, compared to groups with complete and perfectly accurate information (Chapter 3).

Time in patch – The plots in Figure 6.3 show the average length of time spent in a patch by foraging groups. Foragers spend less time in patches as groups increase in size, as we would expect. There appears to be no consistent difference between groups experiencing increasing values of either p or Q. Groups suffering Mistakes (Figure 6.3a) spend noticeably more time in a patch, than those suffering Misses (Figure 6.3b), although this difference becomes trivial in the largest groups.

Patch quitting ability – The plots in Figure 6.4 display the average realised prey quitting values, for foragers attempting to quit patches at optimal C, showing that once again there is no obvious consistency between increasing values of either p or Q, and the realised GUN. Miss groups quit patches when an average of 60 to 120 prey remain, while Mistake groups quit patches when between 100 and 140 prey remain. These do not change as group size increases. Figure 6.5, displaying the coefficient of variation of patch quitting values, demonstrates that groups suffering Misses are able to quit patches relatively consistently in small groups and for low values of p (Figure 6.5a). As both group size increases, and the value of p increases, the CoV also increases and patch quitting becomes more erratic. Groups suffering Mistakes (Figure 6.5b) on the other hand, quit patches more inconsistently in smaller groups, but become more consistent as group size increases.

Figure 6.6 shows the difference between the realised optimal value of C when it is subtracted from the GUN – this gives a measure of how well the foraging group were able to quit patches at optimal C. The higher this difference, the earlier foragers quit patches. For both Misses and Mistakes, as p and Q increase respectively, foragers quit patches progressively earlier. As an increasing number of errors are made a forager's estimate of patch quality becomes more and more inaccurate and they quit patches increasingly earlier. Large groups tend to reduce this and as group size increases groups suffering both Misses and Mistakes quit closer to optimal C than small groups.

Mistake groups quit patches later than Miss groups, harvesting them to a lower prey level. In the previous results section I suggested that foragers making Mistakes would be encouraged to remain in food patches longer because receiving false prey capture signals would lead them to believe that a patch is richer than it really is. The results displayed in Figures 6.4, 6.5 and 6.6 contradict this, and in fact suggest that they will quit patches earlier with an increasing number of false signals. This seems irrational. Foragers making Mistakes think that the patch is richer than it really is. But they also know that there is only an average of 250 items in a patch, so although they are initially encouraged to quit a patch later, they in fact quit earlier once they estimate that they have deplete it more quickly.

Overall, animals experience a decrease in long-term foraging success when they share information that is incomplete or unreliable. They are misinformed as to the true value of a food patch, and cannot accurately estimate the decreasing patch quality. Making false capture signals has more serious ramifications than missing signals of capture events that have really happened, although for a reason different than predicted.

DISCUSSION

In this chapter I examine how the use of public information affects the long-term foraging success of individuals feeding in cohesive groups, when this information is inaccurate or incomplete. The results obtained from simulations using this model show that as the accuracy and reliability of information decreased, foragers suffered depressed foraging success as a result. I examined two types of error likely to occur under natural foraging scenarios: Misses (public information is not effectively transferred to other individuals in the group) and Mistakes (when false information is transmitted). The results here show that each of these types of error affect the ability of foragers to estimate patch quality, which leads them to allocate their patch time inefficiently, with an overall lowering of prey capture rates. Misses occur when a food item is found by an individual but not signalled to other individuals in the group. Thus the forager finding prey can adjust its estimate accordingly, but the other foragers will remain misinformed. This kind of error may occur because foragers are dividing their attention between several personal tasks, and not necessarily focussing

on what other foragers are doing, or they may simply be too far away and not paying attention. Alternatively, a forager finding a prey item may not be concerned with advertising it – I assume here that a prey capture signal is given as an intrinsic part of the feeding process, but as a result it might not be a clear signal and may be easily missed. Misses are also likely to be heavily dependent upon the dynamics of the group. Fernandez-Juridic and Kacelnik (2004) report that starlings pay less attention to the foraging activity of foragers the further away they are. They suggest that this is because it is more costly to obtain this information, but also likely to be of lower relevance to the receiver. In large groups, or where individuals are spread out over a wide area, these signals may also be simply lost through interference by other foragers or factors in the environment (Metcalfe, 1984; Poysa, 1994; Fernandez-Juridic et al, 2004c; Klauer and Zhao, 2004).

The results presented here show that missing public information signals is detrimental to foraging activity, but its effect is only small when considered on its own. The nature of the foraging environment envisioned here is that prey resources exist within either very rich or very poor, but finite (and therefore depleting) food patches. This means that a forager's estimate of patch quality decreases with the amount of time spent feeding in a patch. The longer a forager waits between finding prey items, the poorer it assumes the patch to be. In previous models I showed that when foragers shared information of prey capture events they were able to formulate an accurate estimate of the decreasing patch quality, (Chapter 3), since each individual had access to a greater wealth of up-to-date patch information. But here, some of this information is not communicated to all foragers and so they do not have accurate up-to-date information of patch depletion. Their patch estimate continues to decrease as if no prey ahve been found – the difference being that they actually have found prey, albeit unbeknown to them. Because patches tend either to be rich in prey or nearly devoid of prey, this is not hugely disadvantageous to the foragers. Providing the error rate is not very high it is quite likely that the group will remain in a patch long enough to discover prey that the group acknowledges, and missing out on some prey information does not harm them too much.

On the other hand making false prey capture signals when no prey had been found is extremely detrimental to long-term foraging success. In an environment like the one

modelled here, prey is either very abundant or nearly absent, and so a forager finding prey immediately assumes that it has found a rich patch. It wants to stay there because it believes that the patch must contain many prey. The more prey is found, the more there must be available. Signalling prey capture events that did not occur misinforms the rest of the group about the availability of prey, and they are led to believe that they are in a rich patch when in fact they aren't. Since false signals can be made at any time, it is not at all dependent upon prey actually being present – foragers may choose to remain in a patch for a time, which contains no prey at all. However, foragers are aware of the distribution of prey throughout the environment and roughly how many they are likely to find in each patch. Although they think the group is finding prey more successfully, they are also aware that the patch is being depleted more quickly. Hence, the group decides to quit patches progressively earlier as the rate of false signals increases.

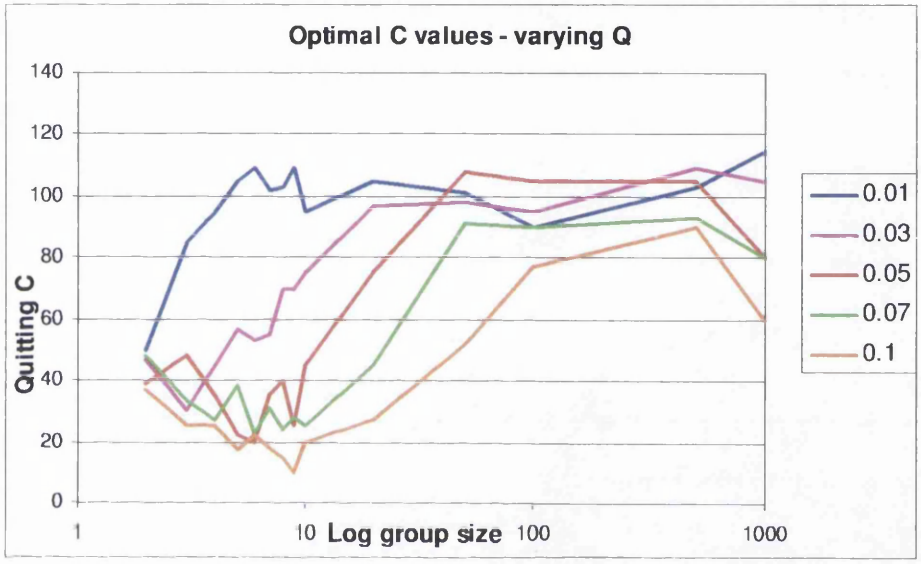
I assume in this model that a forager will either make a false signal, or make a signal that is misinterpreted as something else or is altogether missed. Thus all other members of the group suffer the consequence of this action/-inaction. Making false signals may not be all that unlikely in nature. Or at least receiving them might not be. Evans et al (1993b) state that chickens can become confused by the origin of an approaching predator, by its size and speed. The chickens gave vocal alarm signals for aerial predators when they were approached by fast moving ground predator, and gave non-vocal responses for ground predators when approached by a large aerial predator. Sherman (1985) reported a similar case with Belding's ground squirrel. An animal may learn that a given set of cues (called a template) signifies danger, and anything that matches those cues initiates the same response (Sherman et al, 2001). Thus it is not inconceivable that some completely benevolent action or sound made by a forager may be misconstrued as a prey capture signal. In this case it is quite possible that every individual in the group will make the same mistake.

In contrast it is perhaps not always realistic to suppose that all individuals in a group will miss a signal if it is given. Surely *some* of the foragers will notice a signal, especially if they are close to the signaller. In this model I do not take into account the effect of spacing and distance between individual foragers in a group, and the effect this may have on the transmission of signals between them. I simply assume an

overall error rate for the entire group. Although this may not be entirely accurate it is a reasonable simplification for this model. Some authors suggest that animals do not even pay attention to the activities of all other members of a group, but only those closest to themselves (Elgar et al, 1984; Lima and Zollner, 1996; Couzins et al, 2002; Fernandez-Juridica and Kacelnik, 2004). Fernandez-Juridic et al (2004c) examined the effect of visual perception on the transfer of anti-predator information in animal groups. This model focussed on the scanning frequency of an individual rather than on information fidelity, in a similar way to a previous model of ours (Chapter 5). Further work combining these two approaches, investigating the transmission of information between individuals within groups and the limitations of perception and attention on information acquisition, would prove immensely useful in future. This would allow us to more fully examine the effect of group geometry and dynamics on the accuracy of public information use, and in turn the effect of this on foraging groups, at an individual level. The indications from this Chapter are that this is an important and interesting issue.

Figure 6.1 – Optimal patch quitting values (optimal C) for foraging groups sharing inaccurate information of available food resources. **a)** Varying rates of Mistakes (Q): 0.01, 0.03, 0.05, 0.07, 0.1. **b)** Varying probability of Misses (p): 0.7, 0.8, 0.9, 0.95, 1.

(a)



(b)

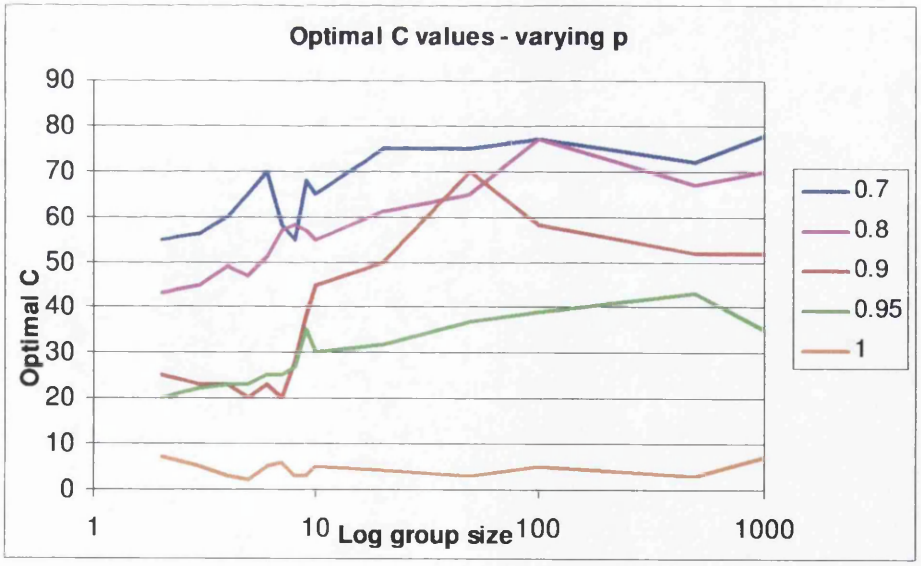
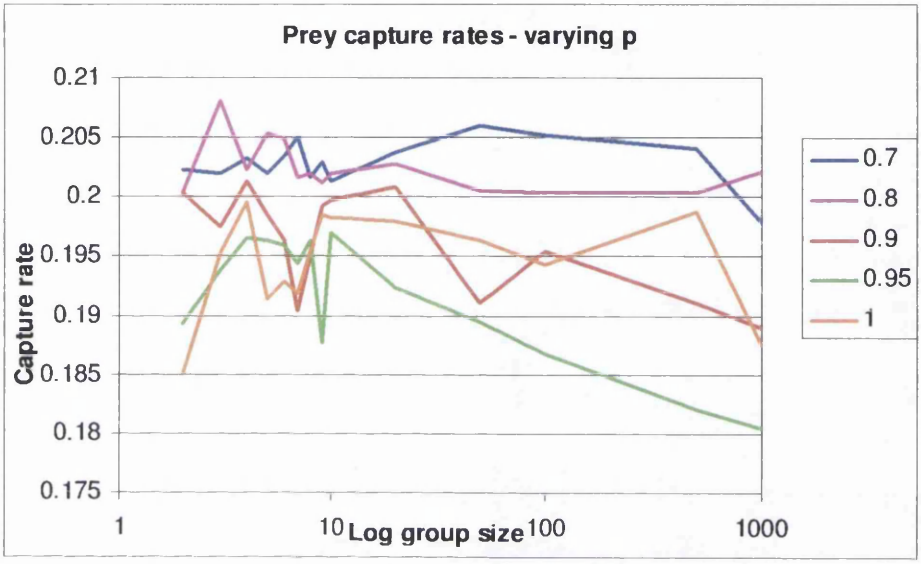


Figure 6.2 – Individual prey capture rates of foragers sharing inaccurate and incomplete public information. **a)** p = probability of missing prey capture signals (Misses). **b)** Q = rate of receiving false prey capture signals (Mistake).

(a)



(b)

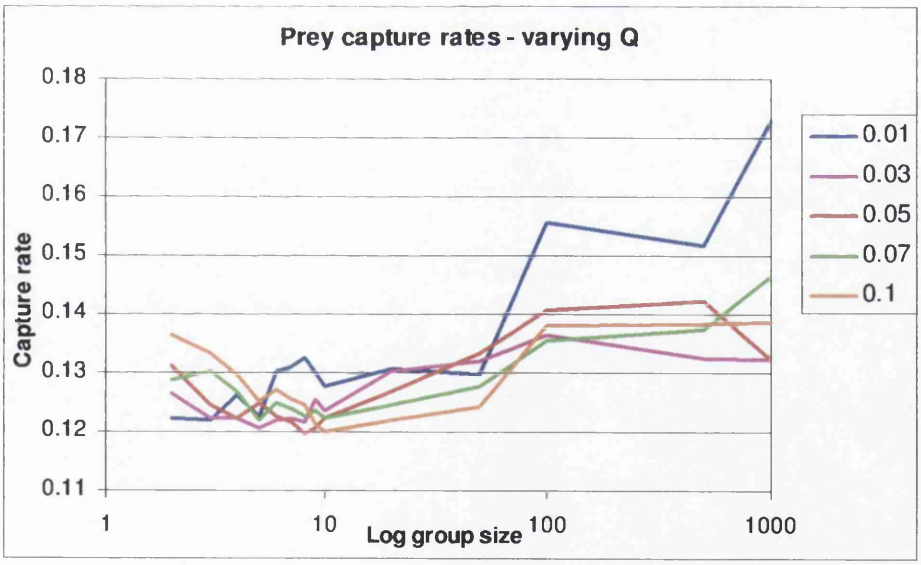
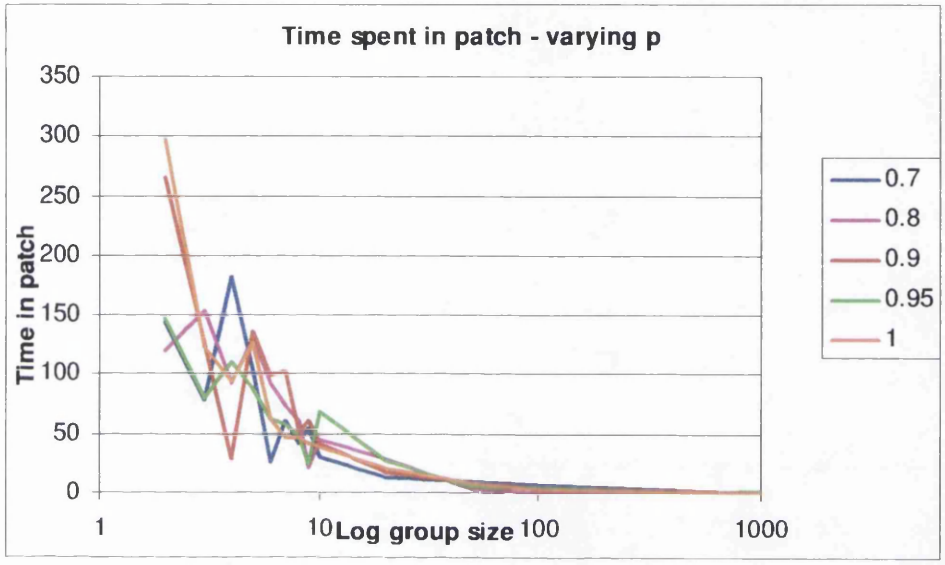


Figure 6.3 – The average time spent in a patch by foraging groups sharing inaccurate and incomplete public information. **a)** p = probability of missing prey capture signals (Miss). **b)** Q = rate of receiving false prey capture signals (Mistake).

(a)



(b)

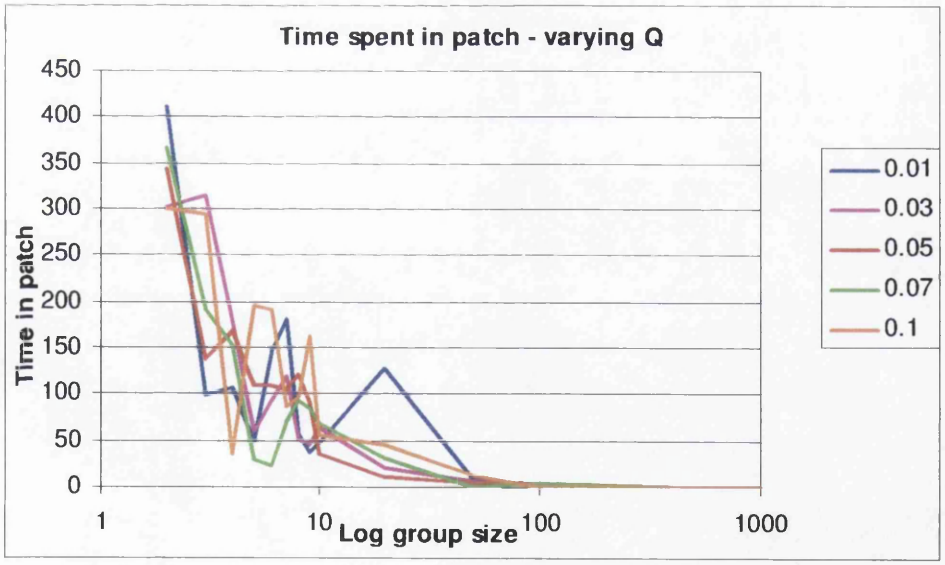
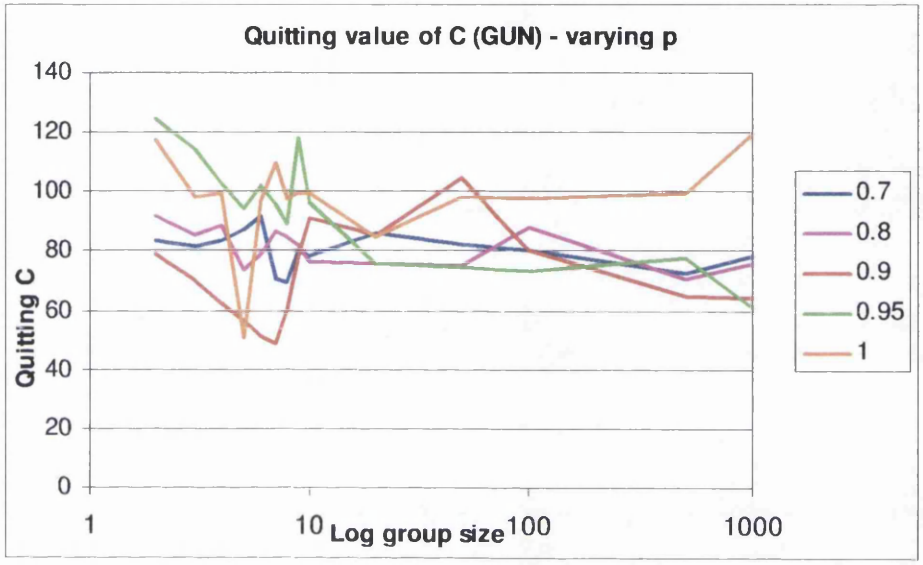


Figure 6.4 – Average prey quitting values (GUN) of foraging groups sharing inaccurate and incomplete public information. **a)** p = probability of missing prey capture signals (Miss). **b)** Q = rate of receiving false prey capture signals (Mistake).

(a)



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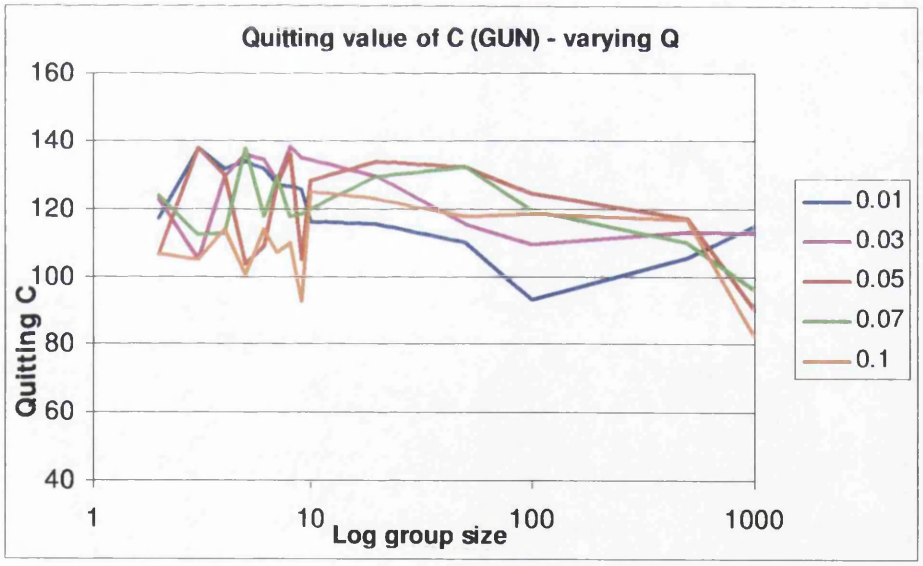
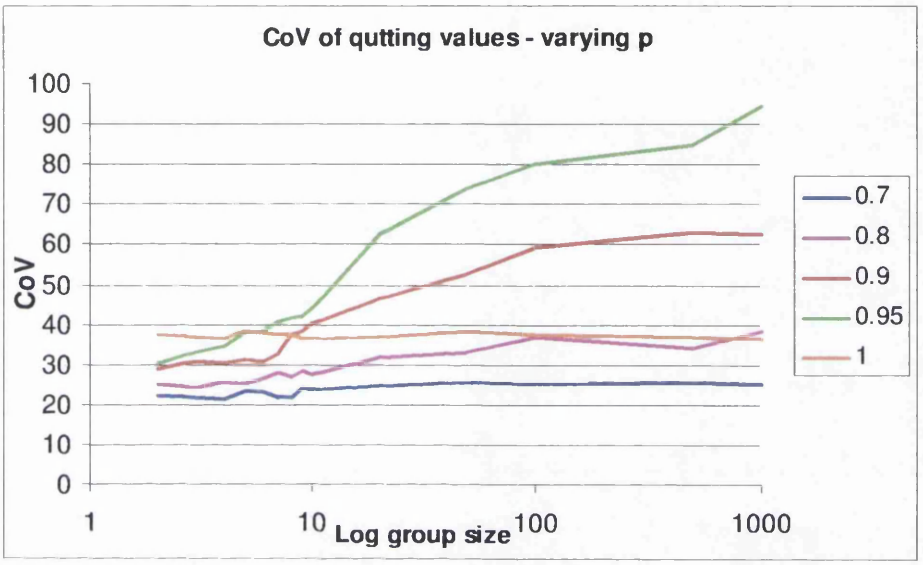


Figure 6.5 – Coefficient of variation of prey quitting values (GUN), for foraging groups sharing inaccurate and incomplete public information. **a)** p = probability of missing prey capture signals (Miss). **b)** Q = rate of receiving false prey capture signals (Mistake).

(a)



(b)

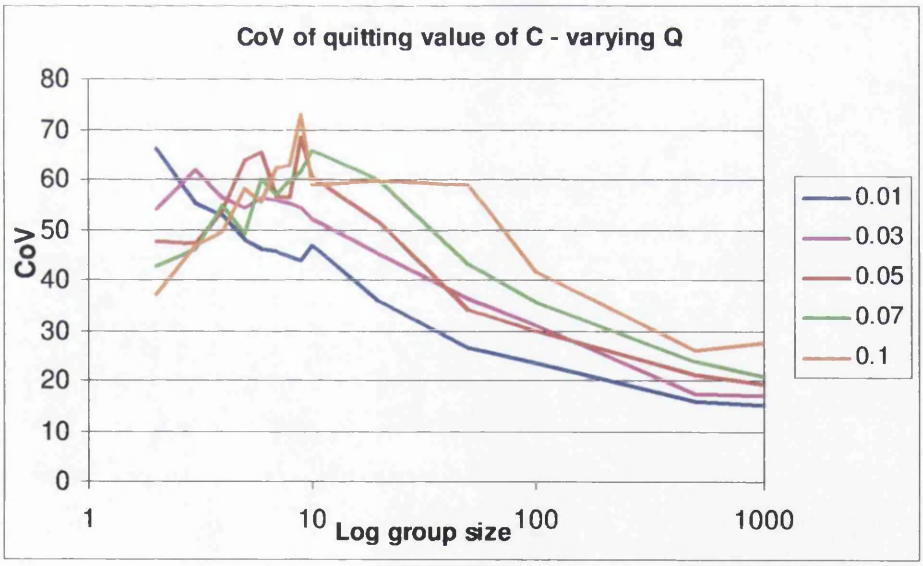
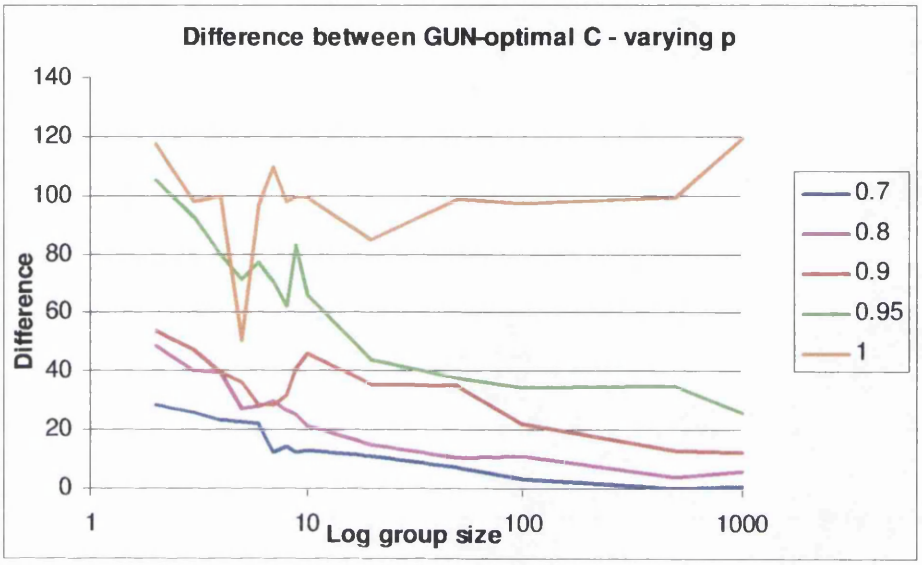
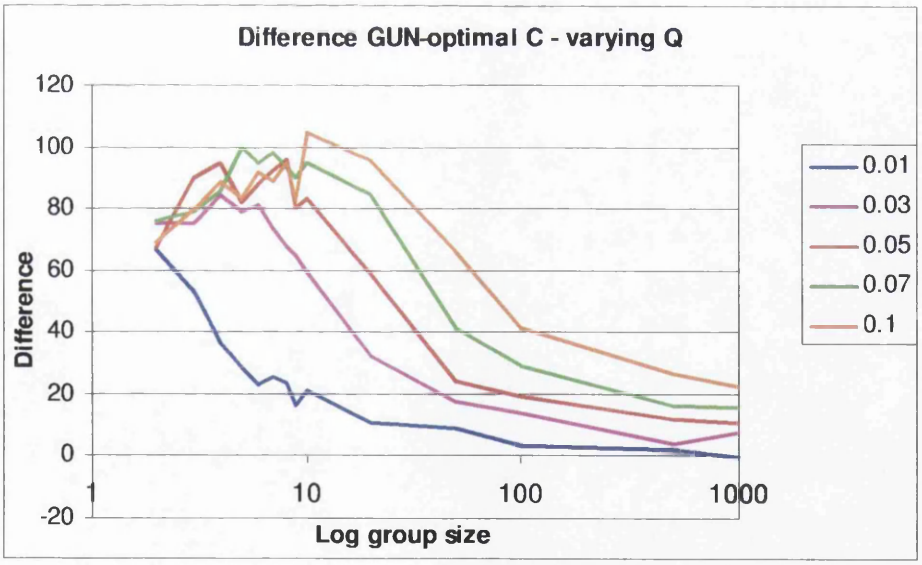


Figure 6.6 – Difference between GUN-optimal C, of foraging groups sharing inaccurate and incomplete public information. **a)** p = probability of missing prey capture signals (Miss). **b)** Q = rate of receiving false prey capture signals (Mistake).

(a)



(b)



CHAPTER 7

AN EVOLUTIONARILY STABLE JOINING POLICY FOR GROUP FORAGERS

ABSTRACT

For foragers that exploit patchily distributed resources that are challenging to locate, detecting discoveries made by others with a view to joining them and sharing the patch may often be an attractive tactic, and such behavior has been observed across many taxa. If, as will commonly be true, the time taken to join another individual on a patch increases with the distance to that patch, then we would expect foragers to be selective in accepting joining opportunities: preferentially joining nearby discoveries. If competition occurs on patches, then the profitability of joining (and of not joining) will be influenced by the strategies adopted by others. Here we present a series of models designed to illuminate the evolutionarily stable joining strategy. We confirm rigorously the previous suggestion that there should be a critical joining distance, with all joining opportunities within that distance being accepted and all others being declined. Further, we predict that this distance should be unaffected by the total availability of food in the environment, but should increase with decreasing density of other foragers, increasing speed of movement towards joining opportunities, increased difficulty in finding undiscovered food patches, and decreasing speed with which discovered patches can be harvested. We are further able to make predictions as to how fully discovered patches should be exploited before being abandoned as unprofitable, with discovered patches being more heavily exploited when patches are hard to find: patches can be searched for remaining food more quickly, forager density is low, and foragers are relatively slow in travelling to discovered patches.

INTRODUCTION

So far in this thesis we have made the assertion that animals searching for food patches are able to find them at a rate that is inversely proportional to the size of the group they are in; so for example a group of 10 individuals will find a new patch in $1/10^{th}$ of the time that is would take a lone forager to do so. We have also assumed that animals forage in tightly cohesive groups, so that when a food patch has been discovered all individuals both enter and leave it as one unit. Both of these assumptions are useful simplifications for the models we have been using thus far, but are not necessarily ecologically realistic. In the natural world foragers searching for food patches are likely be widely dispersed over a given area within the environment, and so when a patch is discovered it is unrealistic to imagine that all individuals will be able to travel to and enter the new patch simultaneously. Assuming all individuals travel at the same speed, those that are very far from the new patch will take longer to travel to it than those that are closer.

Furthermore, since food is not replaced once it is discovered a forager joining a patch later will acquire a smaller share of the patch, because it will already have been partially exhausted by those individuals arriving earlier. Thus, it may be less costly for those individuals that are further away to continue searching for their own patch, than it would be to travel a long distance and join a newly discovered patch that has been partially depleted. The further a forager is from a newly discovered patch, the more costly it will be to travel there, and the lower its share will be from it. There is thus some critical distance at which the benefits from joining a new patch and continuing to search are equal. In this section, we use game theory to find this critical distance. Foragers within this critical distance should join the discovered patch; those further away should continue searching for their own patch. This is the optimal joining strategy.

Patch joining behaviour has been the subject of extensive theoretical work (see Giraldeau and Caraco 2000, and refs. therein), and has been reported in numerous non-human species (see Giraldeau and Beauchamp 1999 and refs. therein). Models

of joining behaviour are typically classified as either information-sharing or producer-scrounger models: information-sharing models assume that foragers are able to search for joining opportunities and undiscovered food patches simultaneously, whereas in the second type these activities are mutually exclusive. Much of the scientific literature has focused on producer-scrounger models, because the benefits of the "producer" and "scrounger" are dependent on the frequency with which they are played in the local population. Girardeau and Beauchamp (1999) argue that in its simplest form the information-sharing model has rather less interesting behaviour, because where there is no cost to scouting for joining opportunities (in terms of interference with personal search ability) the only stable strategy is to join at every opportunity because, nothing is gained by refraining from joining when others join.

Conversely, Ruxton (1995a) and Ruxton et al. (1995) note that the predictions of an information-sharing model should become more interesting if space is considered explicitly. When introducing a cost to joining, in terms of the time spent travelling to discovered patches, we must also take into account the level of patch depletion by the individual discovering the patch and any other individuals that arrive there before the focal forager. This travel time will reduce the value of the patch to a forager further away. Hence, both Ruxton (1995a) & Ruxton et al. (1995) suggest that we should in fact expect flexible behaviour from individuals in an information-sharing situation. They suggest that individuals should only take heed of joining opportunities close to them, and ignore those further away.

In this chapter we present a spatially-explicit analytical model that can be used to generate quantitative predictions of a flexible joining policy within an information-sharing scenario, and how joining behaviour is likely to be influenced by qualities of the foragers and their environment. We do this by building three models. In this first, we summarise the optimal behaviour of a single individual in an environment with food patches that are challenging to find and exhaustible. We then introduce a model in which there are several individuals, but our focal forager is presented with a single joining opportunity, and which no other foragers can take advantage of. The key function of this second model is to help develop insights and methodology that are then used in the more-complex final model that relaxes the simplifying

assumption of the previous model that the foragers are rare, and produces predictions regarding an evolutionarily stable flexible joining policy.

MODEL DESCRIPTION

Single forager

The first scenario we should examine is that of a lone forager. We imagine that a food patch has been discovered and at the time of discovery has a food value of V. Within a patch, prey resources are not replaced once eaten and so deplete over time, thus the gain rate of a forager decreases over time. We can use the differential equation

$$\frac{dV(t)}{dt} = -\alpha V(t)$$

to show that the value of the patch, V(t) at time t in the patch is equal to $V e^{-\alpha t}$ where α is the rate of finding food. According to optimal foraging theory, there is an optimal point in time at which to quit a food patch, in order to maximise long-term prey capture rates (Charnov, 1976; Iwasa et al 1981; Valone, 1993; also see previous chapters). Suppose that our forager chooses to leave the patch when its value has fallen to v. The time at which this occurs is given by

$v = V(t) = Ve^{-\alpha t}$, and thus

$$\frac{v}{V} = e^{-\alpha t}$$

$$\Rightarrow -\alpha t = \ln\left(\frac{v}{V}\right)$$

$$\Rightarrow t = \frac{1}{\alpha}\ln\left(\frac{V}{v}\right). \qquad (1)$$

The reward a forager receives from a patch can be determined as follows:

$$\text{Reward} = \frac{\text{Total value of patch} - \text{Value of patch at quitting}}{\text{Time in patch} + \text{Inter-patch travel time}}$$

or $\frac{V-v}{t+E}$,

and hence $\frac{V-v}{\frac{1}{\alpha}\ln\left(\frac{V}{v}\right)+E}$, (2)

where E is the average time spent between leaving one patch and finding another.

Rate maximisation and patch quitting

We want to find the quitting value, v, which maximises prey capture rates, denoted by v*. Since the capture rate is itself a function of v, we can use the differential formulation

$$\frac{d}{dv}\left(\frac{f(v)}{g(v)}\right)=\frac{g(v)\frac{d}{dv}f(v)-f(v)\frac{d}{dv}g(v)}{g(v)^2}$$

where g = E+1/α(lnV-lnv), and f = V-v, to find the value of v, (v*), for which

$$\frac{d}{dv}\left(\frac{(V-v)}{E+\frac{1}{\alpha}(\ln V-\ln v)}\right)=0. \quad (3)$$

The derivative $\frac{df}{dv}=-1$ and $\frac{dg}{dv}=-\frac{1}{\alpha}\frac{1}{v}$, and so

$$(g(v))^2\frac{d}{dv}\left(\frac{f(v)}{g(v)}\right)=\left(E+\frac{1}{\alpha}\ln V-\frac{1}{\alpha}\ln v^*\right)\times-1+(V-v^*)\left(+\frac{1}{\alpha}\frac{1}{v^*}\right),$$

i.e.

$$-\left(E+\frac{1}{\alpha}\ln V-\frac{1}{\alpha}\ln v^*\right)+\frac{V-v^*}{\alpha v^*}=0. \quad (4)$$

We can rearrange this to show that

$$-E-\frac{1}{\alpha}\ln V+\frac{1}{\alpha}\ln v^*-\frac{1}{\alpha}+\frac{1}{\alpha}\frac{V}{v^*}=0$$

$$\Rightarrow -\alpha E - \ln V + \ln v^* - 1 + \frac{V}{v^*} = 0$$

$$\Rightarrow \frac{V}{v^*} + \ln \frac{v^*}{V} = 1 + \alpha E,$$

which can also be written as

$$\frac{V}{v^*} - \ln \frac{V}{v^*} = 1 + \alpha E. \tag{5}$$

Note that this means that

$$\ln \frac{V}{v^*} = \frac{V}{v^*} - 1 - \alpha E. \tag{6}$$

This gives the quitting value of a forager that will maximise its long-term prey intake rate. It is easy to show that there is only one solution to equation (6), for any given set of parameter values. Figure (7.1) demonstrates graphically, that although both functions of the equation (lnV/v and V/v-1-αE) increase, they do so at different rates, and intersect only once – this intersection being the solution to equation (6). We can also see that as either E or α increase, V/v* also increases and thus v* decreases – our forager should remain longer on a patch with increasing searching rate within a patch, and with the time spent finding a patch. Increasing the value of α increases the instantaneous prey capture rate, thus making patches more profitable for relatively longer for the amount of food it contains. By increasing E, foragers pay a higher cost travelling to a patch, and therefore a patch must be exploited more fully to compensate for the additional cost.

The intake rate of a forager quitting patches at v* can be calculated by simply modifying equation (2):

$$\frac{V - v^*}{E + \frac{1}{\alpha} \ln\left(\frac{V}{v^*}\right)} = \frac{V - v^*}{E + \frac{1}{\alpha}\left(\frac{V}{v^*} - 1 - \alpha E\right)}$$

$$= \frac{\alpha(V - v^*)}{\frac{V}{v^*} - 1}$$

$$= \frac{\alpha(V - v^*)}{\frac{1}{v^*}(V - v^*)} = \alpha v^*. \qquad (7)$$

and hence the prey capture rate is αv^*.

Equation (6) is versatile because although it does not give us exact values of v* for a given patch size, it gives a value which represents the proportion of a patch that should remain on quitting, and thus can be applied to a wide range of initial patch sizes - all we need to do is define the prey discovery rate, α. Figure 7.2 shows plots of ln V/v* values obtained during simulations for a lone forager experiencing different values of (α), for a range of time-to-patch travel costs (E) 1 to 1000.

In all cases, the quitting value of a patch decreases as the cost travelling to it increases. This is consistent with optimal foraging theory (Charnov, 1976; Cowie, 1977; Oaten, 1977; Green, 1980; 1988; and also Chapter 3). This decrease also becomes relatively smaller, as E increases. We can similarly see that as the rate of prey-discovery (α) increases, the V/v* values are lower and their curve decreases more steeply, indicating that the optimal patch-quitting value becomes larger (i.e. foragers should stay a relatively shorter time) when patches are more profitable – this too agrees with classical optimal foraging theory.

Multiple foragers

We now imagine a situation where there is another forager in the environment, and it has discovered a food patch. Our focal forager now faces a choice – it can join the discovered patch or it can continue searching for its own. For the sake of simplicity we concentrate on only one joining opportunity - we do this because if our forager can join patches on several occasions its overall prey capture rate will be higher and this notation will be slightly inaccurate. We also assume that no other foragers exist

in the environment and that no subsequent patch joining opportunities will arise in the future.

Suppose that at time 0 our forager stands at distance x from the patch that has just been discovered. It has a speed of travel denoted by S, and so its time to the patch will be x/S, and the value of the patch when it arrives is V(x/S). We want to find the value of x at which the prey intake rate of the forager is equal to that if it simply continued searching for its own patch, denoted by x_c. A food patch, once found by another forager, will have a food value of $V_x = Ve^{-\alpha x/s}$ by the time our forager arrives there, having travelled from distance x. As soon as our forager enters the patch, the feeding rate in the patch increases to 2α because now the patch contains our focal forager as well as the individual that discovered it. Since

$$\frac{d}{dt}V_x(t) = -2\alpha V_x(t)$$

the value of the food patch at time t, (since the arrival of the joiner) is $V_x(t) = V_x e^{-2\alpha t}$.

Now let us suppose that our forager aims to leave the patch when its value has decreased to $V_x(t) = v_x$. At this time, our forager has acquired $0.5(V_x - v_x)$ food, and has spent time t in the patch, where

$$v_x = V_x e^{-2\alpha t}$$

$$\Rightarrow 2\alpha t = \ln\left(\frac{V_x}{v_x}\right)$$

$$\Rightarrow t = \frac{1}{2\alpha}\ln\left(\frac{V_x}{v_x}\right). \qquad (8)$$

If we include with this the time spent travelling to the patch, x/S, we can see that the feeding rate of our forager for this particular trip is

$$\frac{0.5(V_x - v_x)}{\frac{x}{S} + \frac{1}{2\alpha}\ln\left(\frac{V_x}{v_x}\right)} = \frac{V_x - v_x}{2\frac{x}{S} + \frac{1}{\alpha}\ln\frac{V_x}{v_x}}. \qquad (9)$$

In order to maximise feeding rates a forager should join a patch that has been discovered by another individual, only if its feeding rate for doing so would be higher than the long-term average, αv^*. If it is lower than this value, the forager would be better off searching for its own patch. We want to find the value of v_x, (v_x^*) at which the foraging rate is maximised, i.e.

$$\frac{d}{dv_x}\left(\frac{V_x - v_x}{2\frac{x}{S} + \frac{1}{\alpha}\ln\frac{V_x}{v_x}}\right) = 0 \quad . \tag{10}$$

It is worth a forager joining a patch if and only if their foraging rate exceeds the average feeding rate, αv^*. The maximum feeding rate occurs at the level v_x, which satisfies

$$1 + 2\alpha\frac{x}{S} = \frac{V_x}{v_x^*} - \ln\frac{V_x}{v_x^*},$$

(leading on directly from equation (6)), giving a prey intake rate of αv_x^*. A forager should only join a patch that has been discovered if $v_x^* > v^*$. v_x^* is given by

$$1 + 2\alpha\frac{x}{S} = \frac{V}{v_x^*}e^{-\alpha x/S} - \ln\left(\frac{Ve^{-\alpha x/S}}{v_x^*}\right)$$

$$\Rightarrow 1 + 2\alpha\frac{x}{S} = e^{-\alpha x/S}\frac{V}{v_x^*} - \ln\left(\frac{V}{v_x^*}\right) + \alpha\frac{x}{S}$$

$$\Rightarrow 1 + \alpha\frac{x}{S} = e^{-\alpha x/S}\frac{V}{v_x^*} - \ln\left(\frac{V}{v_x^*}\right). \tag{11}$$

We already know that it is best for a forager to join a patch when it stands at a distance below the critical value x_c, ($x < x_c$) – it is not worth foragers joining a patch if they are further away than this critical distance. The lower this distance, x, the more attractive patch joining will become. Since v^*_x is the optimal value of v for a forager to quit a patch, when at a given distance x, v^*_{xc} is thus the optimal value of v for a forager to quit a patch when at the critical distance, x_c. Leading on from equation (6) again, we can see that

$$\ln\left(\frac{V}{v^*}\right)=\frac{V}{v^*}-1-\alpha E$$

and

$$\ln\left(\frac{V}{v^*_{xc}}\right)=e^{-\alpha x_c/S}\frac{V}{v^*_{xc}}-1-\alpha\frac{x_c}{S}.$$

Since $v^*_{xc} = v^*$, we can re-write this as:

$$\frac{V}{v^*}-1-\alpha E=e^{-\alpha x_c/S}\frac{V}{v^*}-1-\alpha\frac{x_c}{S}$$

$$\Rightarrow\frac{V}{v^*}-\alpha E=e^{-\alpha x_c/S}\frac{V}{v^*}-\alpha\frac{x_c}{S}$$

$$\Rightarrow\frac{V}{v^*}\left(1-e^{-\alpha x_c/S}\right)=\alpha\left(E-\frac{x_c}{S}\right)$$

$$\Rightarrow\frac{v^*}{V}=\frac{1-e^{-\alpha x_c/S}}{\alpha\left(E-\frac{x_c}{S}\right)}, \qquad (12)$$

where v^* is given by equation (6). We could find v^* using (6) specifying E, α and V. Combining the two equations (6) and (12) allows us to calculate the value of x_c providing S is also specified. We can now see that $x_c < ES$, and thus $E > x_c/S$. In other words, a forager should not travel further to a discovered (and thus partially depleted) patch than to a previously undiscovered patch.

Note that if $\frac{\alpha x_c}{S}$ is small,

$$\frac{v^*}{V}\approx\frac{\alpha\frac{x_c}{S}}{\alpha\left(E-\frac{x_c}{S}\right)}$$

$$\Rightarrow\frac{v^*}{V}\approx\frac{\frac{x_c}{S}}{\left(E-\frac{x_c}{S}\right)}$$

$$\Rightarrow\frac{x_c}{S}\approx\frac{v^*}{V}E-\frac{v^*}{V}\left(\frac{x_c}{S}\right)$$

$$\Rightarrow x_c \approx \frac{v^*/V}{1+v^*/V} ES . \qquad (13)$$

Finding the critical patch-joining distance

Taking the values of V/v_x^* obtained for each combination of α and E in equation (6), we entered these into a computer model written to solve equation (12) – we call this the Joiner model. Although we had obtained V/v_x^* using particular values of α and E we could set V/v_x^* as a separate parameter into Joiner, thus allowing us to vary α and E again within each simulation, so we can examine the effect of each on the critical patch-joining distance. We took the V/v_x^* values for each combination of α and E value (E = 4, 10, 40, 100, 200, 400, 500, 600, 700, 800, 900,1000; α = 0.01, 0.02, 0.03, 0.05, 0.1) from equation (6) and then entered each V/v_x^* value, and its respective E value into Joiner. We then vary α through 0.01, 0.02, 0.03, 0.04, 0.05, 0.06,0.07, 0.08, 0.09, 0.1. For simplicity, and because of its direct and predictable effects on E, we maintained the speed of travel (S) constant at a value of 2. Figure (7.3) shows the plots of x_c values obtained for each of these simulations.

RESULTS

The plots in Figure (7.3) show that, first of all, with increasing inter-patch travel time (E) the critical patch joining distance (x_c) also increases. Each curve on the graphs represents a different value of E, and as E increases in each graph the value of x_c also increases. This is completely intuitive, because it suggests that when patches are far apart, foragers should travel further to get to them – the average travel time is higher and so they do not really have a choice because if they do not travel that distance they'll never join a patch. Since patches are more difficult to find, joining one that has been discovered by another forager will become a more attractive prospect than continuing to search for a fresh one. Similarly, when patches are close together foragers should not be willing to travel further than the nearest patch, because they

will be easier to find themselves and will therefore not have to suffer one that has already been partially depleted.

We can see that, moving through Figures 7.3a-e, the value of x_c increases with increasing prey discovery rate, α. As searching intensity within a patch increases, the patch will be depleted to a lower prey level before our focal forager arrives and thus our forager will find it less profitable, even though its instantaneous prey capture rate will be higher – the result is that it should want to harvest the patch to a lower value of v_x before it quits. However, our forager will also experience higher instantaneous prey capture rates in patches that it discovers itself, and since it will not have to share this bounty with another forager it will find joining a discovered patch less appealing than continuing to search for its own. It will therefore be willing to sustain a higher cost travelling in-between patches because it is worth paying a higher initial cost if the reward is also relatively higher as this will make up the initial cost. When the reward is low a forager should not be prepared to pay a high travel cost, because the reward will not cover it and the forager will be better off not making the effort in the first place.

However, within each figure, it is clear that the value of x_c increases with increasing α. At first this is slightly puzzling, especially since it conflicts with the statement in the previous paragraph. But when considering this it must be borne in mind that α is now out of context with the other parameters used to produce it. The value of vx we enter into the Joiner model already assumes that α, S and E have been defined and finds the x_c for these given values, for which it will be correct. In varying this value of α we are contradicting this assumption and x_c will no longer be 'correct' value for defined value of vx. Thus, we cannot be surprised if the results are not what we'd predict.

Equation (6) shows us that vx is a fixed proportion of V, defined by the parameters E and α, so simply changing V will have no effect on x_c because vx will also change. Our results here show that as the value of V/v_x^* decreases the critical distance to join a patch also decreases – following Figure 7.3a through 7.3e the x_c curves are of a lower value, have a smaller starting value and increase less steeply as the value of α

in equation (6) increases (and thus as V/v_x^* decreases). Since V/v_x^* represents the proportion of a patch that should remain when a forager quits, and a high V/v_x^* is equivalent to low prey density in a patch, this suggests that a forager should harvest patches to a lower level when they travel further to each patch. Similarly, when they only travel a short distance to a patch they should not harvest it to such a low level. This agrees with the predictions of classical foraging theory, and the statement in the previous paragraph.

Multiple foragers, with joining

So far, we have assumed that once our forager finds a patch no others can join it, and so the food is consumed by only two foragers – the one that discovered the patch and our focal forager. It is not difficult to alter this notation to imagine that our forager has joined two or more others that are already at a patch. Now we imagine that all individuals can join a patch. Let us assume that at time 0 our forager stands at a distance x_c from the patch, where x_c is the critical distance at which foragers enter a patch – those closer than this move into the patch, and those further away continue searching. Thus, no others can join a patch after our focal forager. There is one forager already at the patch, and other foragers exist at a density λ throughout the environment. For simplicity we consider a uniform spread of individuals, so that our equations will contain fractions of individuals. The critical distance x_c marks the point at which it becomes equally profitable to join this patch, or to continue searching for others. All foragers assume the same value of x_c and so all individuals within this critical distance join the patch, while all those outside it ignore this patch and thus can be disregarded. Since our forager sits at the distance x_c it will be the last to enter the discovered patch. If we begin at t_0 we define the number of individuals on a patch at any time as Y(t), and the number of individuals arriving at the patch between time t and $t+\delta t$ is $St+S\delta t$, so that within a small length of time, δt, the number of individuals that arrive at the patch (δY) is the number within the radius of circle x_c minus the number in the circle St:

$$\delta Y = \pi\lambda(St + S\delta t)^2 - (St)^2$$

$$= \pi\lambda(2S^2t\delta t + 2S^2(\delta t))$$

$$\pi\lambda 2S^2t\delta t = \lambda\pi\, 2St \times S\delta t \qquad (14)$$

and so Y(t) increases in time δt by

$$\delta y = \lambda\pi 2S^2 t\delta t$$

$$\Rightarrow \frac{d}{dt}Y(t) = 2\pi S^2 t\lambda . \tag{15}$$

Where Y(0) = 1

$$\Rightarrow Y(t) = \int_0^t 2\pi S^2 t\lambda dt + 1 = 1 + \left(\frac{2\pi S^2 \lambda t^2}{2}\right)_0^t = 1 + \pi S^2 \lambda t^2 . \tag{16}$$

Hence, if we substitute t for x_c/S then the number of individuals already on a patch is

$$Y\left(\frac{x_c}{S}\right) = 1 + \pi S^2 \lambda \left(\frac{x_c}{S}\right)^2$$

$$= 1 + \pi\lambda x_c^{\,2} . \tag{17}$$

After this our focal forager arrives into the patch, and the total number of individuals there is now $2+\pi\lambda x_c^2$. The arrival of our forager means that no others will enter the patch. At this point the value of the patch is now $V_{xc,}$ after which, following on from earlier can be written as follows:

$$\frac{dV(t)}{dt} = -\alpha\left(1 + \pi S^2 \lambda t^2\right)V(t)$$

$$\Rightarrow \frac{1}{V(t)}\frac{dV(t)}{dt} = -\alpha\left(1 + \pi S^2 \lambda t^2\right)$$

$$\Rightarrow \frac{d}{dt}\ln(V(t)) = -\alpha\left(1 + \pi S^2 \lambda t^2\right)$$

$$\Rightarrow \ln V(t) = -\alpha\left(t + \frac{\pi\lambda S^2 t^3}{3}\right) + K$$

$$\Rightarrow V(t) = K' e^{-\alpha\left(t + \frac{\pi\lambda S^2 t^3}{3}\right)} . \tag{18}$$

Where t = 0, V(0) = V $\Rightarrow$ K'= V

$$\Rightarrow V(t) = Ve^{-\alpha\left(t + \pi S^2 \lambda \frac{t^3}{3}\right)}$$

$$\Rightarrow V_{xc} = V\left(\frac{x_c}{S}\right) = Ve^{-\alpha\left(\frac{x_c}{S}+\frac{\pi S^2 \lambda x_c^3}{3S^3}\right)} = Ve^{-\alpha\frac{x_c}{S}\left(1+\frac{\pi\lambda x_c^2}{3}\right)}. \quad (19)$$

We will now follow the logic of the previous section to calculate the intake rate of our forager for a single foraging trip. When our forager arrives on a patch its value is V_{xc}. We want to find the time τx, that our forager will spend on the patch if it quits at v_x:

$$v_x = V_{xc}e^{-(2+\pi\lambda x^2{}_c)\alpha t}$$

$$\Rightarrow (2+\pi\lambda x^2{}_c)\alpha t = \ln\left(\frac{V_{xc}}{v_x}\right)$$

$$\Rightarrow t = \frac{1}{(2+\pi\lambda x^2{}_c)\alpha}\ln\left(\frac{V_{xc}}{v}\right). \quad (20)$$

If we include the time spent travelling to the patch, x_c/S, we can see that the feeding rate for exploiting the patch this time is

$$R_x = \left(\frac{1}{\frac{x_c}{S}+\frac{1}{(2+\pi\lambda x^2{}_c)\alpha}\ln\left(\frac{V_{x_c}}{v}\right)}\right)\left(\frac{V_{x_c}-v}{2+\pi\lambda x^2{}_c}\right). \quad (21)$$

Now we want to find the value of v_x, (v_x*) at which the foraging rate (R_x) is maximised, i.e.

$$\frac{d}{dx}\left(\frac{V_{xc}-v_x}{(2+\pi\lambda x^2{}_c)\frac{x_c}{S}+\frac{1}{\alpha}\ln\frac{V_{xc}}{v_x}}\right) = 0 \quad . \quad (22)$$

The maximum feeding rate occurs at the level v_{x*} which satisfies

$$1+(2+\pi\lambda x^2{}_c)\alpha\frac{x_c}{S} = \frac{V_{xc}}{v_x*} - \ln\frac{V_{xc}}{v_x*},$$

$$\ln\left(\frac{Vx_c}{vx*}\right) = \frac{Vx_c}{Vx*} - 1 - \alpha\left(\frac{Xc}{S}\right)\left(2+\pi\lambda x^2{}_c\right) \quad (23)$$

(leading on directly from equation (4) again), giving a prey intake rate of αv_x^*. Substituting for V_{xc} is given by (19).

We must now find the overall long-term prey capture rate of the entire population. This is different from the first two models because other foragers can also take advantage of discovered food patches. Let t_f denote the time spent on a patch for the very first individual to enter – i.e. the instant the patch has been discovered by the first the forager. Thus, t_f is given by

$$t_f = \frac{x_c}{S} + \frac{1}{(1+\pi\lambda x^2{}_c)\alpha} \ln\left(\frac{V_{xc}}{v_x^*}\right). \tag{24}$$

As soon as a patch is discovered, all individuals within distance x_c of the patch travel towards it and so until time t_f after this, are either feeding in the patch or travelling to it. We assume here that patches exist at a low enough density so that none of the zones of radius x_c surrounding each patch overlap. The term $(1+\pi\lambda x^2 c)$ denotes the number of foragers (N) either travelling towards the patch, or already present there, and E denotes the average time spent by one individual travelling to a patch. The average time spent by the group (finding and feeding time) is

$$E + t_f(1+\pi\lambda x^2{}_c) \tag{25}$$

and the amount of food consumed has a value of

$$V - V(t_f) = V - v_x^*. \tag{26}$$

The overall intake rate of the population is thus

$$\alpha v_x^* = \frac{V - v^*}{E + t_f(1+\pi\lambda x^2{}_c)} \tag{27}$$

Since foragers should quit patches when their feeding rate falls to the average rate of the whole population, the optimal feeding rate αv_x^* is also described by (27).

By substituting for t_f using equation (23), and Vx_c using equation (19) we find another relationship between x_c and v_x^*:

$$\left(\frac{\alpha v_x^*}{V}\right)\left(E - \frac{x_c}{S}\right) = 1 - \exp\left(-\frac{\alpha x_c}{S}\left(1 + \frac{\pi\lambda x_c^2}{3}\right)\right). \tag{28}$$

Combining equations (23) and (28) we arrive at

$$\frac{V}{vx^*} - \ln\left(\frac{V}{vx^*}\right) = 1 + \alpha E + \left(\frac{2\alpha\pi\lambda x_c^{\,3}}{3S}\right). \qquad (29)$$

We can solve equations (23) and (28) to find vx and x_c, specifying λ, α, E, S and V. Comparison with (4), demonstrates that since x_c must be positive, then v_x* must be less than v* for a single forager, and the long-term food uptake rate is always lower for an individual foraging with others than for one able to exploit the same environment on its own. The reason for this is the time spent in travelling to join discovered patches. Despite this, it is not advantageous to entirely give up joining if others will still join your discoveries, and similarly in a population of non-joiners an individual that switched to joining and sharing nearby discoveries would do better than non-joining individuals, so joining is the evolutionarily stable strategy for selfish individuals, even though not joining would yield higher long-term reward rates if such a strategy could be cooperatively adopted and maintained.

We can imagine a natural ecological situation where this model might be used to predict patch-joining behaviour of group foragers. Let us imagine a flock of birds searching an area of grassland for small clumps of snails or earthworms. We set our parameter values at V = 100, E = 10, λ = 0.01, S = 5, α = 0.05. Thus, we assume that all food patches are equal and have a starting value of 100KJ. Foragers searching for a patch will take on average 10 seconds to find one, and to travel to it, moving at a speed of 5 metres per second. Foragers exist uniformly throughout the environment at a density of $0.001m^{-2}$, and thus there are an average of 10 foragers within any 100x100m square. After arriving on a food patch the initial rate at which food is consumed is 5KJ per second. Snails and earthworms yield an approximate energy density of 3KJ per gram, and so each patch contains 30g of prey.

Our third model, called Multiple-Joiner, solves equations (24) and (29) simultaneously, giving us values for both vx and x_c for a given set of parameter values. Following the example in the previous paragraph Multiple-Joiner gives us xc = 13.5284 and vx = 40.8711. Since the speed of travel between patches is 5 ms^{-1} this predicts that foragers will be willing to travel upto 13.5284 / 5 = 2.70568 seconds in

order to join a patch that has been discovered by another individual. Once a patch has been discovered it will be harvested to just above 40% of its initial value before foragers should quit and continue searching for others – foragers consuming 100 – 40.8711 = 59.1289KJ of prey from it, which is roughly equivalent to 20g or snail or earthworm.

We can see that the average long-term prey capture rate of a forager in this joining environment is $\alpha v x^* = 2.044$. Equation (6) shows us that the long-term prey capture rate for a lone forager (i.e. when $\lambda = 0$) would have been 2.12073.

Finding the critical patch-joining distance

By setting λ at 0 (i.e. no other foragers) we can test this model against the previous Joiner model, comparing the results of both. Results obtained from several runs using Multiple-Joiner are consistent with those of Joiner, for a range of α (and thus V/v_x^*) values.

RESULTS

Using the Multiple-Joiner model we can investigate the effect of each of the parameters α, λ, E, S and V, on the critical patch quitting values (v_x^*) and their respective patch joining distances (x_c), of a forager feeding in an environment similar to that described above. We maintain these parameters at constant default values, varying one at a time over a wide range of values.

We can determine that varying the initial size of a foraging patch, V, will have no effect on either v_x^* or x_c. As noted earlier, we can see from equation (6) that v_x^* is not a fixed, specified value of prey but rather a proportion of a patch that is remaining. Changing the value of V will alter the value of prey at which foragers should quit the patch (t_f and thus also v_x^*) but the ratio of V/v_x^* will not change and all patches will be equally profitable. Similarly, because all patches begin with the

same value V, and thus also have the same value of v_x*, the critical joining value, x_c, will not differ because no patch will be more attractive than another. Figures 7.4a and 7.4b demonstrate this clearly – here we vary V between 1 and 500, the result being that both v_x* and x_c remain constant for all values.

The prey capture rate of foragers, however, does change with V – Figure 7.4c shows that as the initial patch value increases the intake rate of both lone foragers and those in a group will also increase. As V increases, the amount of food available to foragers increases, and so patches become more profitable to foragers in both situations – this is completely intuitive. We can also see from Figure 7.4c that lone foragers experience gradually, but progressively higher prey capture rates than those feeding in a group. Since the available prey resources in a patch will be shared between several foragers within a group, lone individuals should be expected to experience higher rewards than those in groups, for any given value of v_x* and x_c.

Next, we vary the speed at which foragers travel to a patch (S). Figures 7.5a and b shows that as S increases x_c (and thus the distance at which a forager will be willing to join a patch) also increases while decreasing the length of time a forager will be willing to spend within each patch (t_f). We assume there is no energetic cost to increasing S and so if a forager can travel faster to a patch that is further away, it will become more attracted to it, the result being that the value of x_c in general will increase. Because it is now easier to travel to discovered patches, the amount of time spent feeding in each one will be lower due the ease at which a new one can be found – note that a low time in patch (t_f) is generally equivalent to a high value of v_x*. Figure 7.5c suggests that a forager in a group will experience an overall decrease in long-term capture rates, because all foragers will find discovered patches similarly attractive and so food resources will again be shared between a larger number of individuals. A lone forager will see no such decrease. S does not affect the capture rate of a lone forager because it only governs the speed of approach to a patch once it has already been discovered. This will never happen when a forager is alone - it will always take time E to reach a patch and so the total foraging time will not change.

As the time taken for a forager to travel to a discovered patch (E) increases, the attractiveness of patches are increased – indicated by an increasing x_c (Figure 7.6a).

Where E is large, patches are harder to find, and so travelling to one that has been discovered is more profitable than continuing to search for a new one. Foragers must therefore also harvest patches to a lower v_x^* (increasing t_f) because they are harder to come by (Figure 7.6b). We can see from Figure 7.6c that a forager both on its own and in a group will experience a decreasing long-term prey capture rate. Since varying E affects the extent to which a patch is harvested, and thus v_x^*, the capture rate for both is altered.

We can see from Figure 7.7a that as we increase the density of foragers (λ), and thus the number of foragers near to a discovered patch, that the value of x_c decreases. When λ is high there will be more individuals sharing any discovered patches, and so the amount of food resources each forager acquires will be lower (Figure 7.7c). Although patches will be discovered with a higher frequency, more time will be spent travelling to them collectively, resulting overall in a lower foraging efficiency. Each patch will be harvested for a smaller length of time (high v_x^*) because it is relatively easy to find another, more profitable patch elsewhere (Figure 7.7b). Since more foragers will be sharing any discovered patch when λ is high, each forager will obtain a smaller portion of food from it and so will be less willing to travel there – it may be more beneficial for them to find their own, as yet undepleted patch. However, since there will be more foragers in the vicinity of this new patch, it will remain profitable for a shorter time, leading to a decreasing prey capture rate as λ increases.

Now we vary the searching rate within a patch (α). As α increases, foragers will be finding prey resources in a patch more easily, and therefore an increase in prey capture rates (Figure 7.8c). Since food will be consumed from a patch more quickly before a forager reaches a patch, it should not be willing to travel so far to get to one that has been discovered – indicated by a low x_c (Figure 7.8a). But because each patch is more profitable once a forager has arrived there, and because the overall long-term prey capture rate increases, the time spent exploiting a patch will decrease (Figure 7.8b).

DISCUSSION

In this chapter we have produced the first quantitative predictions for a flexible joining strategy in situations that are well described by the information-sharing hypothesis. The results displayed here confirm the previous suggestion that there should be a critical patch joining distance, with all joining opportunities to a forager within that critical distance being accepted, and all others being ignored. Results indicate that this distance is unaffected by the total availability of food in the environment, but that it increases with the decreasing density of other foragers, with the increasing speed of movement towards discovered patches, with an increased difficulty in finding undiscovered food patches, and also with a decrease in searching rate in patches which have been discovered.

The models presented here enable us to make predictions as to the extent to which discovered food patches should be exploited, before being abandoned as unprofitable. Patches should be harvested to a lower prey level when patches are hard to find, and when patches can be searched more quickly for remaining food. They should also be harvested to a lower level when forager density is low and foragers are relatively slow in travelling to discovered patches. All these predictions should be easily open to empirical testing. Common species that have been used in laboratory experiments of social foraging are small passerine birds and shoaling freshwater fish (see Krause & Ruxton, 2002 for an overview), searching for experimentally manipulated patches of food distributed in their environment. Both of these groups should be suitable for the study of our predictions of the theory presented here. Previous studies have shown that in both fish (Krause & Godin, 1996) and birds (Templeton & Giraldeau, 1995a and b) characteristic feeding behaviour can be detected by other foragers, even while searching for food themselves, and so the key requirements of the information-sharing hypothesis are likely to be met.

When examining the predictions of a theoretical model, it is important to consider the limitations imposed on it by the assumptions it makes. There are two types of assumptions to consider here: the assumptions of the information-sharing scenario, and further assumptions that we have had to make in our analytic derivations. The

key requirement for foraging situations to be modelled by either producer-scrounger or information sharing models is that food (or any resource) is distributed in patches that are challenging to find (in that foragers cannot go immediately from one patch to the next), that the food is available in such patches that several individuals can feed simultaneously in the same patch, and that feeding leads to depletion of the patch. These conditions are found in many situations occurring in nature. The additional specific requirement of information-sharing models is that an individual's ability to discover food patches is not negatively influenced if they also search for joining opportunities – i.e. they do not incur a cost in searching for their own patches, when scouting for other discoveries. Foragers may sometimes alert other foragers to a discovery that they have made, in order to gain anti-predatory benefits from feeding as a group (e.g. Elgar, 1986a). However, from a foraging viewpoint alone, they should make detection of their food discovery as challenging for other foragers to notice as possible. Having said that, the discoverer will likely have to adopt characteristic behaviours that are different from those associated with searching in order to exploit the food resource themselves, and these characteristic behaviours can often be easily identified by other nearby foragers (e.g. Brockman & Barnard, 1979; Pitcher & Magurran, 1983).

It seems almost inevitable that the demand for sensory processing combined with cognitive limitations would mean that performing an extra task, such as searching for joining opportunities, would lead to at least some partial impairment of their performance at another task, such as searching for undiscovered food. This seems intuitively likely to be dependent on how challenging each task is (Milinksi & Heller, 1978; Dukas & Ellner, 1993; Dukas & Kamil, 2001). Finding previously undiscovered food patches is likely to be challenging because it requires movement around the environment, rather than because it is sensorially challenging (a human example might be searching for your car in a large car park compared with looking for a dropped contact lens). In this case, if we assume that each task does not require a large investment in cognitive processing, then information sharing may be a closer approximation to reality than the mutual-exclusion of producer-scrounger. Evidence of similar multi-tasking has been shown, for example, in flocking birds (Lima, 1995) - these can feed on grains from the substrate and also detect the predator-induced departures of flock-mates (differentiating these from departures for other reasons).

Hence, there is reason to expect that situations that can be explained by the information-sharing hypothesis should actually be relatively common in the natural world. Empirical exploration of the relationship between the efficiency of looking for joining opportunities and undiscovered food patches would be immensely beneficial.

There are further specific assumptions that we have made within this model to gain analytical tractability. Firstly, we assume that foraging activity occurs in a two-dimensional space. Whilst this is likely to be appropriate for many natural systems, especially in terrestrial ecosystems, foraging in the open ocean may well be more appropriately examined as a three-dimensional environment. It should not be too difficult to extend this theory for such a situation, and we would perhaps expect little loss in analytic tractability and or change in our conclusions.

We further assume that when a patch is discovered, nearby foragers are distributed uniformly throughout the environment. This is unlikely to hold true where food patches are relatively densely distributed in the environment (i.e. where the time to find a patch (E) is small). Where patches are close together, the process of joining and then simultaneously dispersing from a patch naturally leads to clumping of individuals. However, after dispersal from a patch, individuals should seek to spread out so as to minimise the risk of searching parts of the environment already unsuccessfully searched by other individuals. Providing food patches are relatively scarce, so that when individuals quit a patch they disperse some distance from it before any of these individuals finds another patch, then our assumption of uniformly distributed foragers may be a fair and realistic.

A further assumption is again one relating to the scarcity of patches. Here we assume that zones of attraction surrounding two patches (i.e. the circles with radius x_c) that are being exploited simultaneously do not overlap. This assumption was introduced to avoid considering more complex strategies involving not only the decision of whether to join a patch or not, but also *which* patch to join from a number of available choices. Again we can see that the key assumption underlying our theory is one of patch abundance. Relaxing the requirement is likely to require numerical simulation methods as well as consideration as to how individuals choose between several available joining opportunities (see Ruxton et al, 1995 for further consideration of

this). It is worth remembering, however, that if patches are relatively easy to find then joining becomes an unattractive tactic, and so our theory is least applicable under conditions where joining is least likely to occur. Furthermore, we expect that our predictions will remain qualitatively intact in simulations that relax the assumptions considered above – this would also be a topic of interest for experimental exploration.

Another consideration that simulation models would have to make is the appropriate search trajectories for a group of individuals simultaneously leaving a depleted patch. We should expect natural selection to have elected foragers that adopt trajectories that minimise the overlap between their individual search fields. Both theoretical (Barta et al, 1997) and laboratory experiments (Flynn & Giraldeau, 2001) have demonstrated that producers and scroungers take up characteristically different positions with respect to other individuals. Scroungers seek to be near the producers so they are in a position to take advantage of joining opportunities; whereas producers prefer to distance themselves in order to allow them as much time as possible to exploit their discoveries before joiners arrive. In information-sharing models where each searching individual can become either a joiner or a discoverer, there is a trade-off between the positions (with respect to other individuals) that are most advantageous to each potential outcome. Hence, the evolutionarily stable for search trajectories and consequent distribution of individuals within the local environment is not obvious and it would be well worth further research. Again, such theoretical work would greatly benefit from simple empirical work that mapped the trajectories of foragers as they leave depleted food patches.

Figure 7.1 – Graph demonstrating the optimal quitting value v (v*) of a patch, maximising long-term capture rates. Following equation (6), the value at which a forager should quit a patch will occur when ln V/v = V/v-1-αE. Since these two functions increase at different rates, there is one and only one solution to this – i.e. when the two intersect.blue line = ln V/v, red line = V/v –1-αE

α = 0.012, E = 400; V = 250

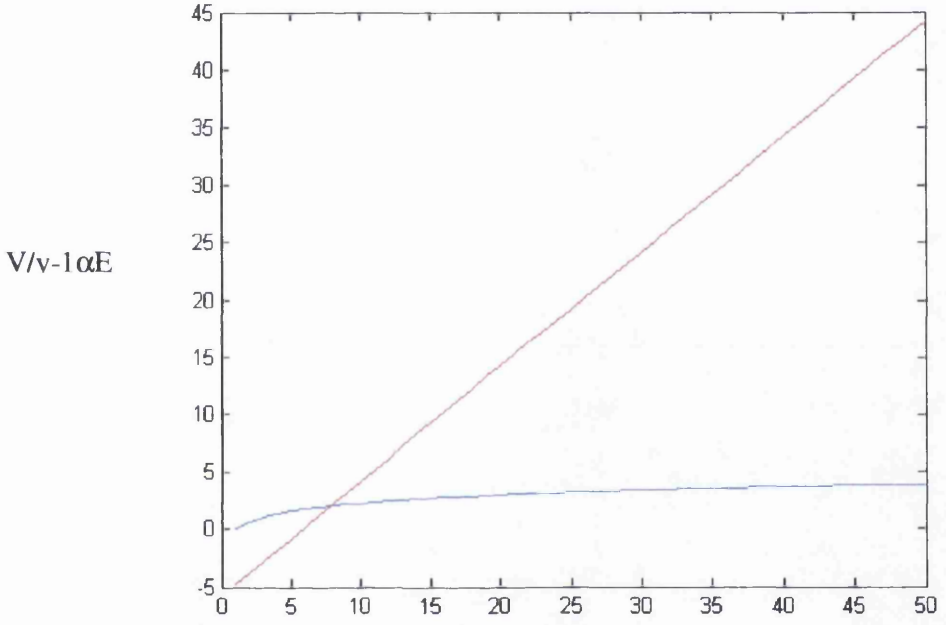
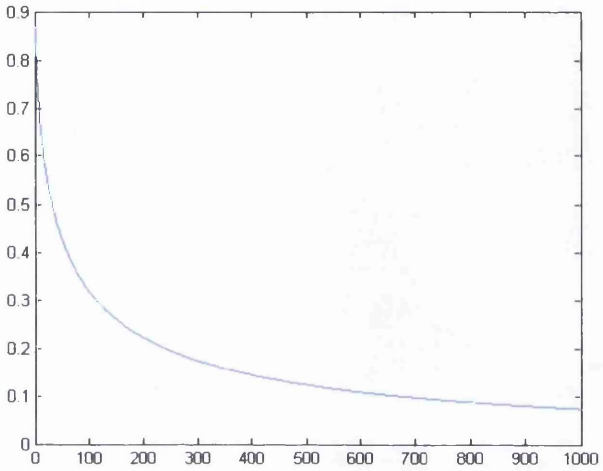
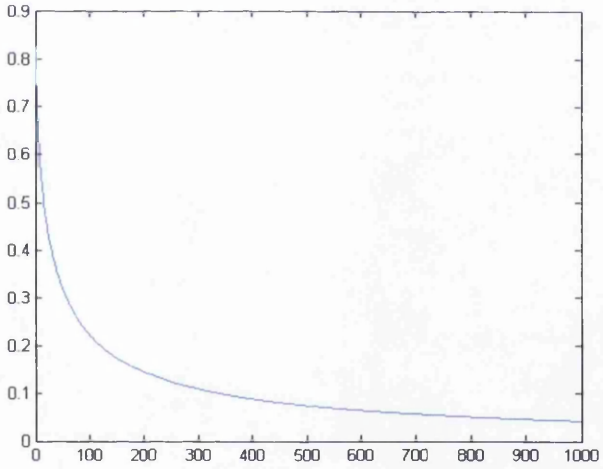


Figure 7.2 – Plots showing values of log V/v*, for inter-patch travel costs 1 to 1000 and prey-discovery rates (α). x-axis = travel cost (E), y-axis = log V/v* **a)** α = 0.01, **b)** α = 0.02, **c)** α = 0.03, **d)** α = 0.05, **e)** α = 0.1.

(a)



(b)



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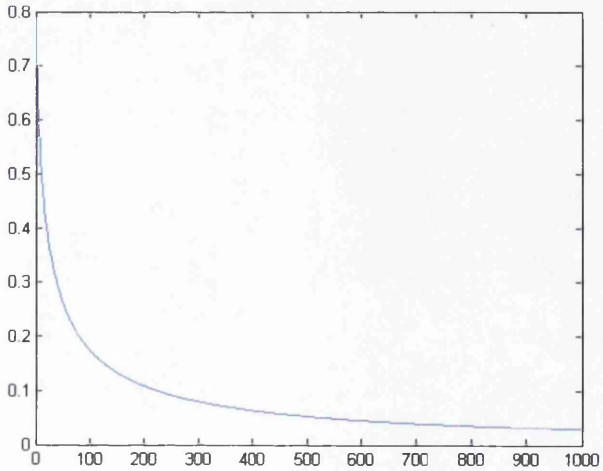
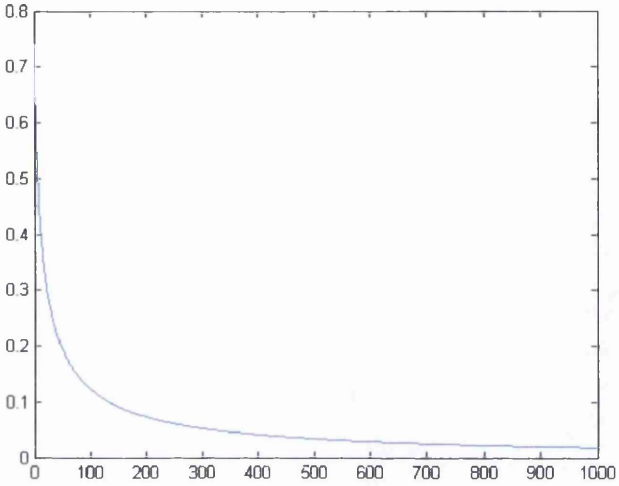
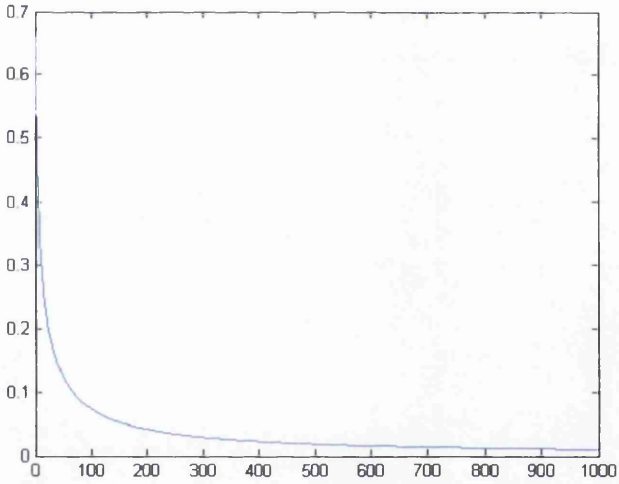


(d)


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
100
200
300
400
500
600
700
800
900
1000

(e)


0.7
0.6
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0.4
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200
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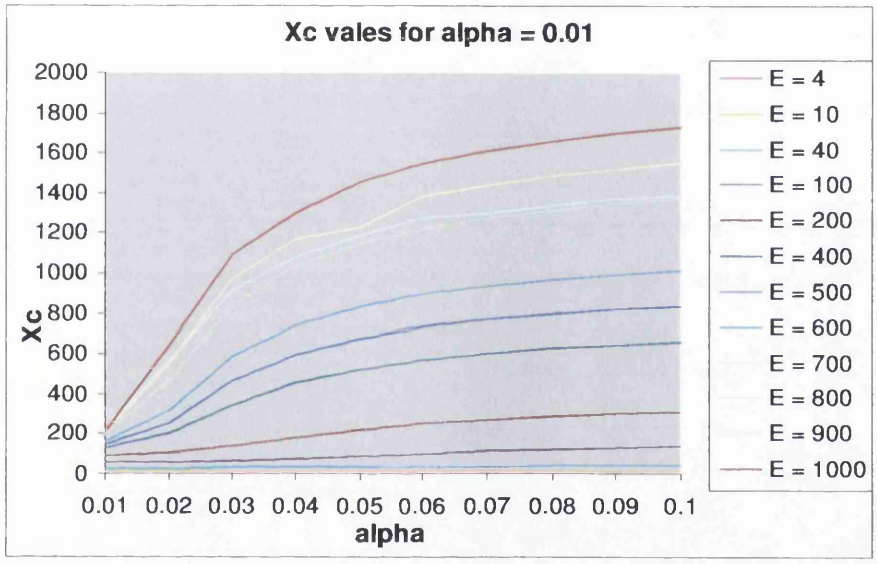
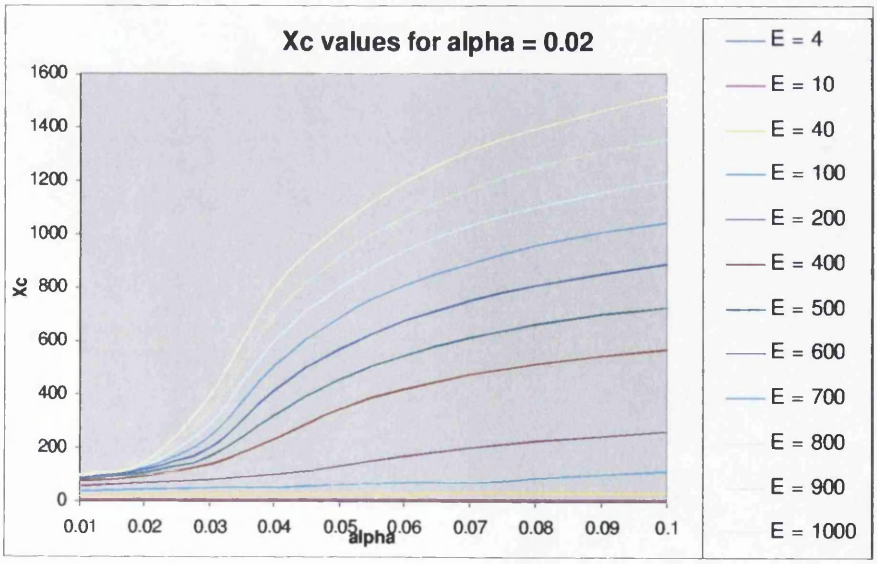
700
800
900
1000

Figure 7.3 – Plots showing critical patch-joining distances (x_c) obtained using the Joiner model, for a range of log V/v* values. The plots show a series of patch joining values that were obtained for given combinations of α and E. There is a specific value of V/v* for each combinatin of α and E, (E = 4, 10, 40, 100, 200, 400, 500, 600, 700, 800, 900, 1000, α = 0.01, 0.02, 0.03,0.04 0.05, 0.06, 0.07, 0.08, 0.09, 0.1) but here we vary the values of both α and E again for each of these V/v*. E is varied within each plot, α is varied over the series of plots. **a)** α = 0.01, **b)** α = 0.02, **c)** α = 0.03, **d)** α = 0.05, **e)** α = 0.1. x-axis = prey discovery rate (α), y-axis = critical patch-joining distance (x_c).

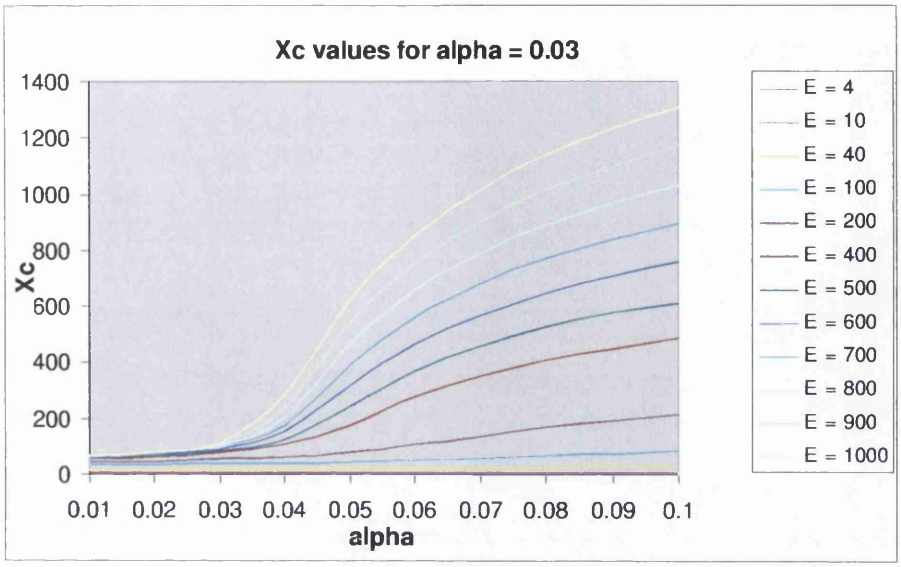


(a)

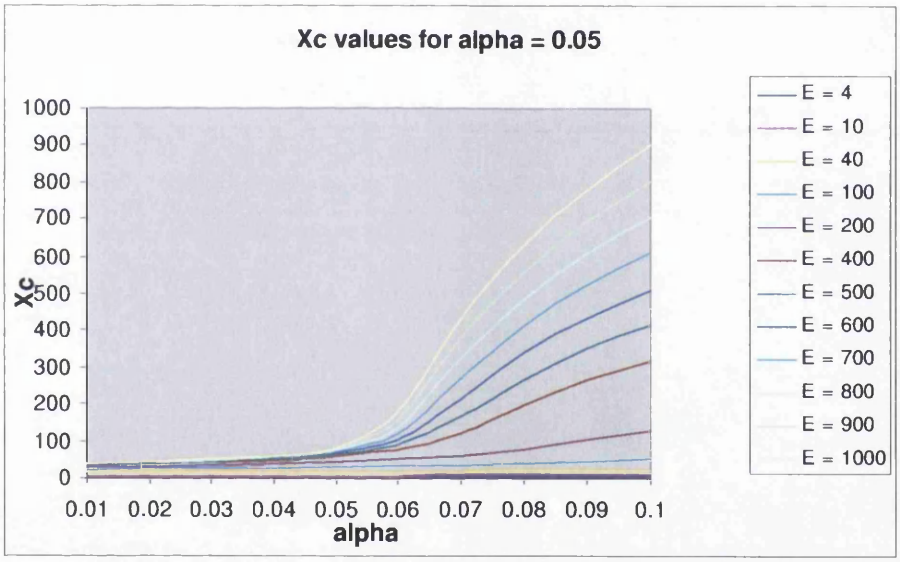


(b)

(c)


Xc values for alpha = 0.03
Xc
alpha
0
200
400
600
800
1000
1200
1400
0.01 0.02 0.03 0.04 0.05 0.06 0.07 0.08 0.09 0.1
E = 4
E = 10
E = 40
E = 100
E = 200
E = 400
E = 500
E = 600
E = 700
E = 800
E = 900
E = 1000

(d)


Xc values for alpha = 0.05
Xc
alpha
0
100
200
300
400
500
600
700
800
900
1000
0.01 0.02 0.03 0.04 0.05 0.06 0.07 0.08 0.09 0.1
E = 4
E = 10
E = 40
E = 100
E = 200
E = 400
E = 500
E = 600
E = 700
E = 800
E = 900
E = 1000

(e)

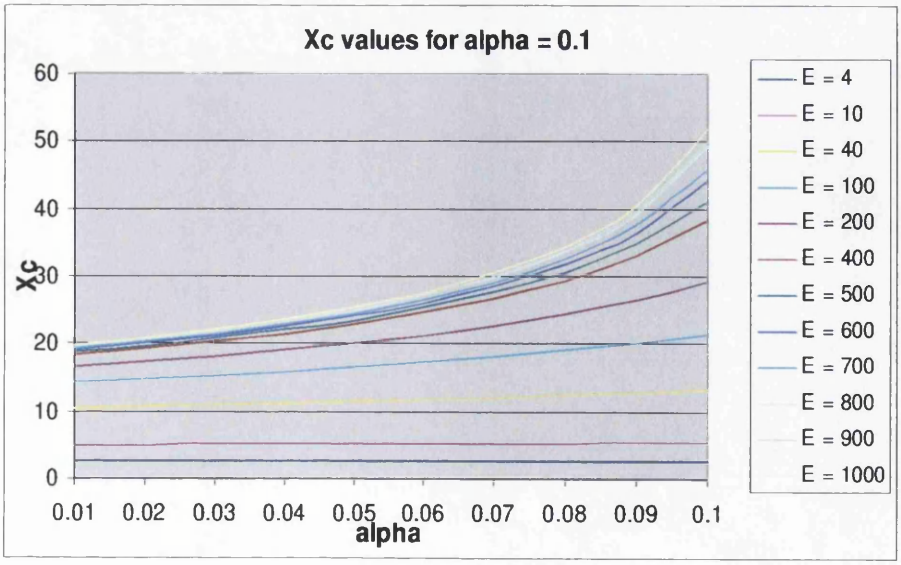
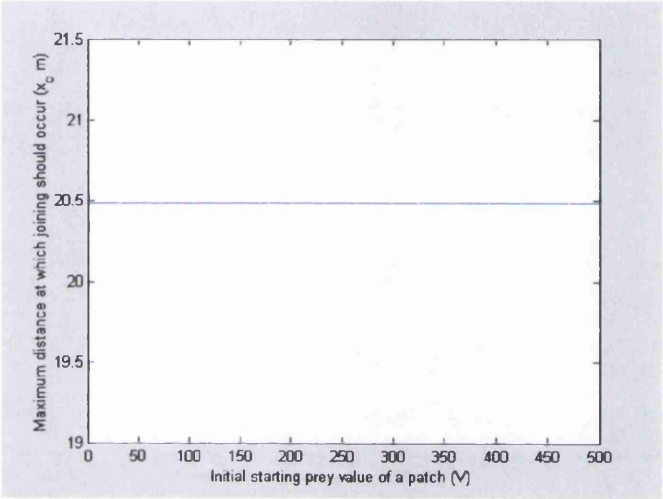
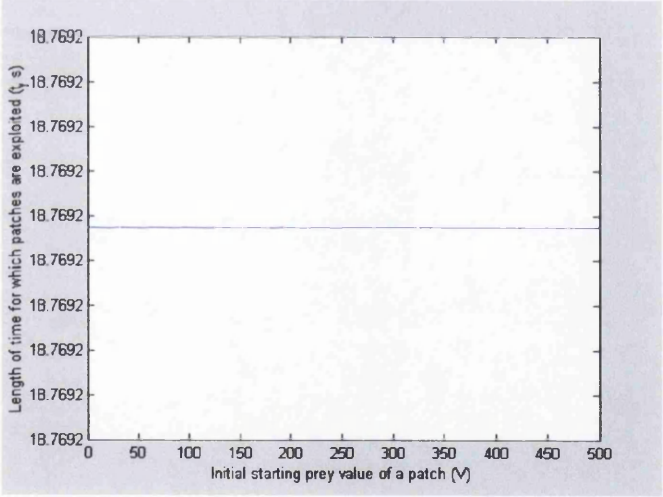

Xc values for alpha = 0.1
Xc
alpha
0
10
20
30
40
50
60
0.01 0.02 0.03 0.04 0.05 0.06 0.07 0.08 0.09 0.1
E = 4
E = 10
E = 40
E = 100
E = 200
E = 400
E = 500
E = 600
E = 700
E = 800
E = 900
E = 1000

Figure 7.4 – Critical patch joining distances, x_c, **(a)** and respective patch quitting values, vx*, **(b)** obtained using Multiple-Joiner model - where all individuals can also join a discovered patch – for a range of initial patch values, V (V = 1:500). All other parameters remain constant: E = 100, α = 0.05, λ = 0.001, S = 2. Also displayed are the long-term prey capture rates **(c)** of both a lone forager in such an environment, and a forager in a group with other individuals at a density of 0.001.

(a)



(b)



(c)

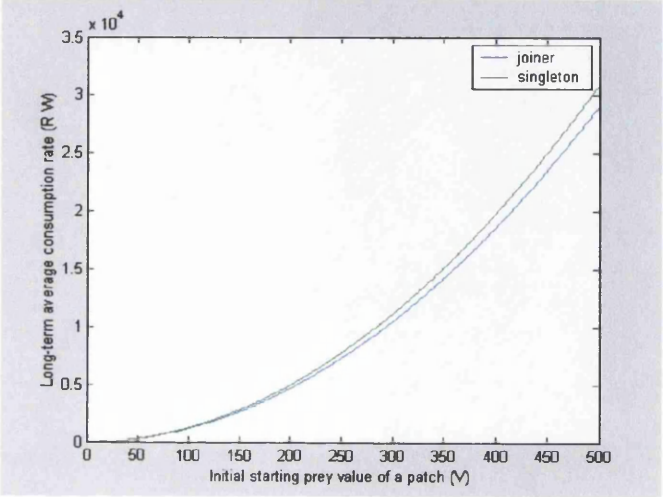
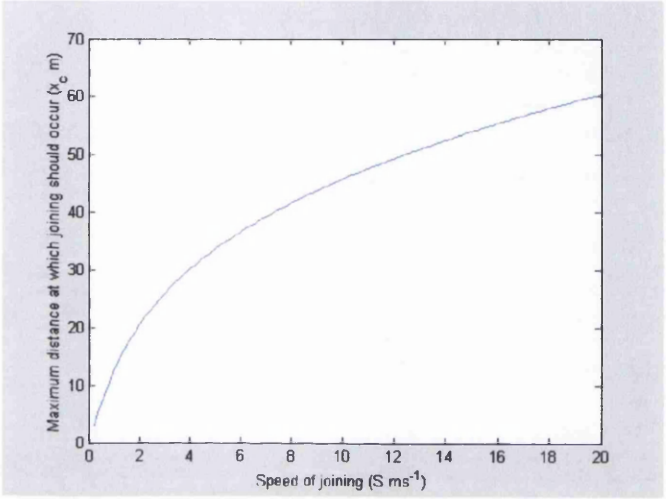
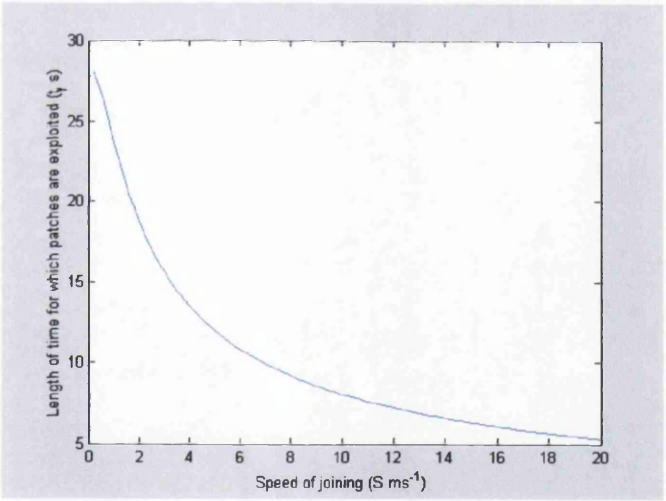


Figure 7.5 - Critical patch joining distances, x_c, **(a)** and respective patch quitting values, v_x*, **(b)** obtained using Multiple-Joiner model - where all individuals can also join a discovered patch – for varying between patch travelling speeds S (S = 0.2:20). All other parameters remain constant: E = 100, $\alpha = 0.05$, $\lambda = 0.001$, V = 277. Also displayed are the long-term prey capture rates **(c)** of both a lone forager in such an environment, and a forager in a group with other individuals at a density of 0.001.

(a)



(b)



(c)

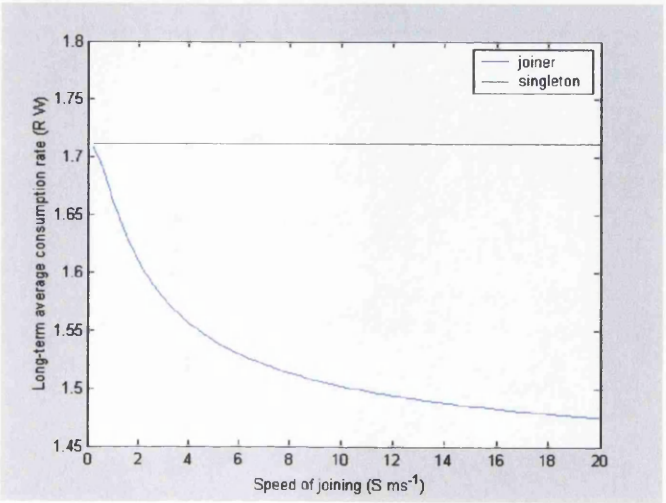
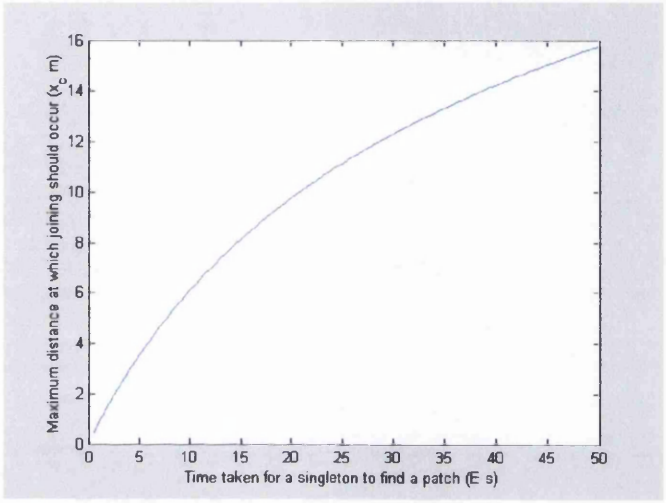
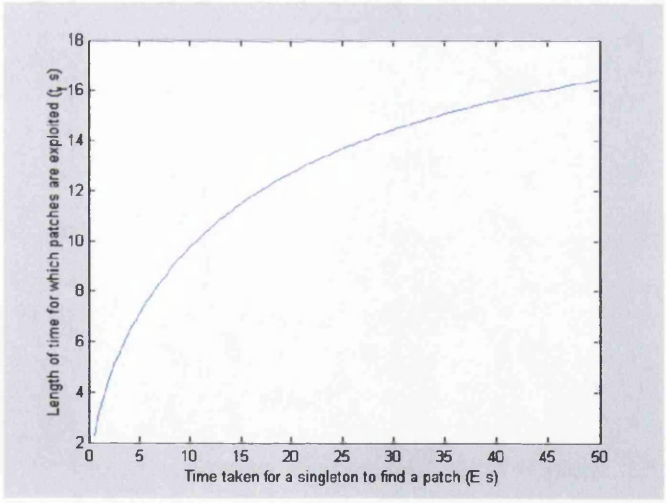


Figure 7.6 - Critical patch joining distances, x_c, **(a)** and respective patch quitting values, v_x*, **(b)** obtained using Multiple-Joiner model - where all individuals can also join a discovered patch – for varying average travelling times E (E = 0.5:50). All other parameters remain constant: $\alpha = 0.05$, $\lambda = 0.001$, S = 2, V = 277. Also displayed are the long-term prey capture rates **(c)** of both a lone forager in such an environment, and a forager in a group with other individuals at a density of 0.001.

(a)



(b)



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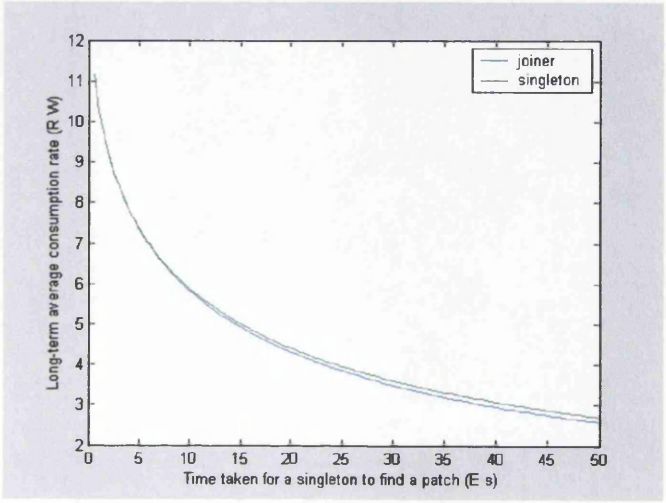
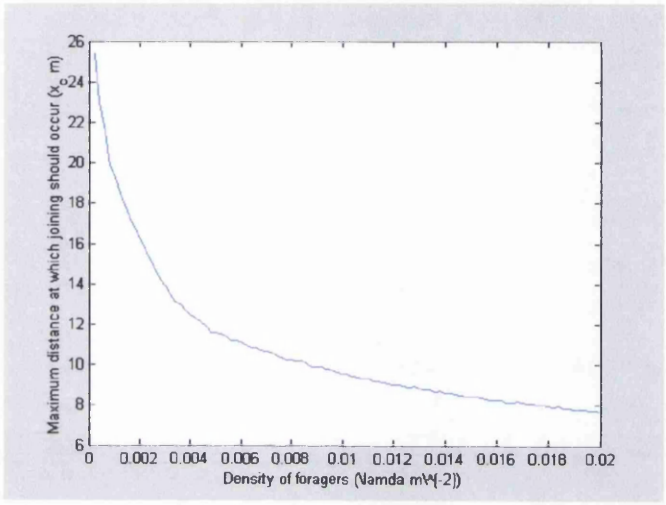
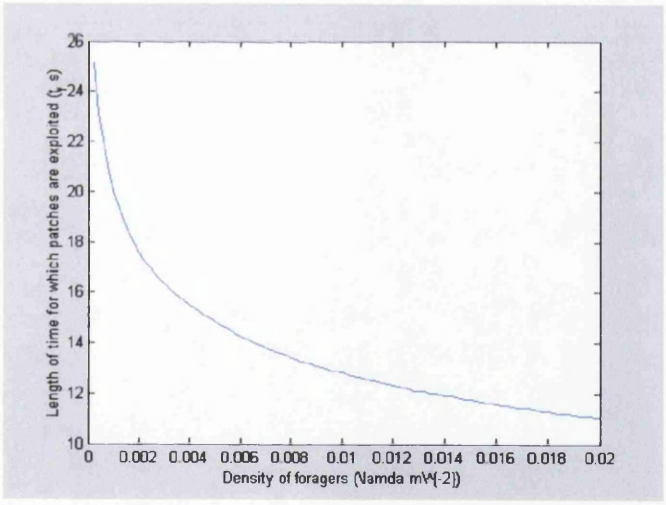


Figure 7.7 - Critical patch joining distances, x_c, **(a)** and respective patch quitting values, v_x*, **(b)** obtained using Multiple-Joiner model - where all individuals can also join a discovered patch – for varying forager densities λ (λ = 0.0002:0.02). All other parameters remain constant: E = 100, α = 0.05, S = 2, V = 277. Also displayed are the long-term prey capture rates **(c)** of both a lone forager in such an environment, and a forager in a group with other individuals.

(a)



(b)



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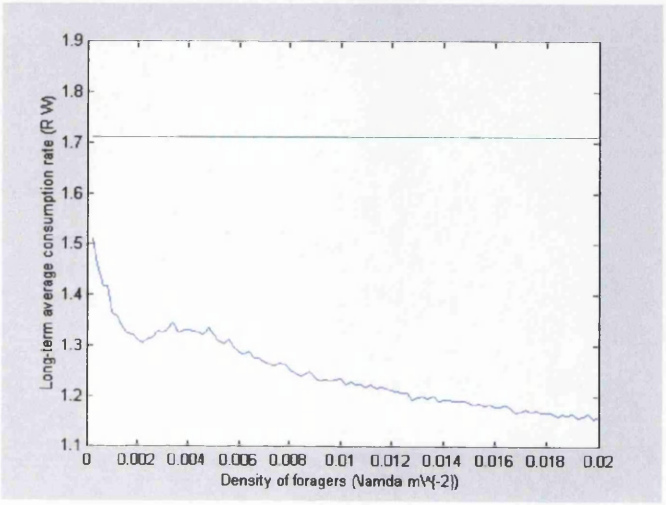
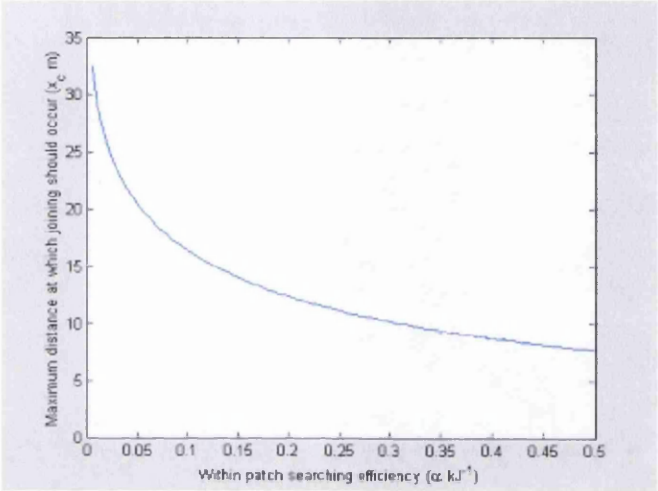
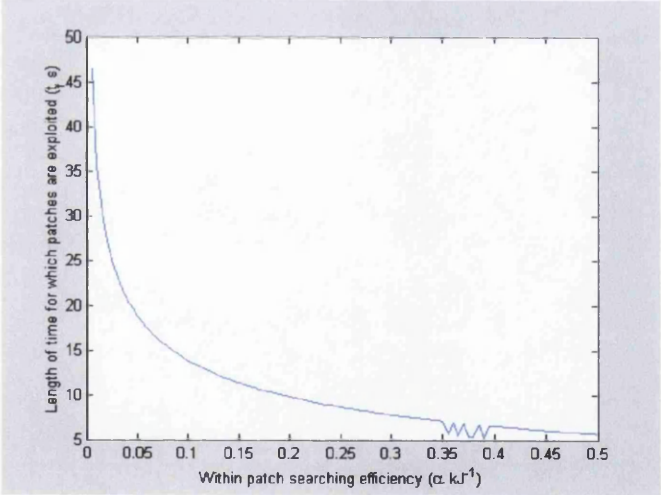


Figure 7.8 - Critical patch joining distances, x_c, **(a)** and respective patch quitting values, v_x*, **(b)** obtained using Multiple-Joiner model - where all individuals can also join a discovered patch – for a range of within patch searching rates α (α = 0.05:0.5). All other parameters remain constant: E = 100, λ = 0.001, S = 2, V = 277. Also displayed are the long-term prey capture rates **(c)** of both a lone forager in such an environment, and a forager in a group with other individuals at a density of 0.001.

(a)



(b)



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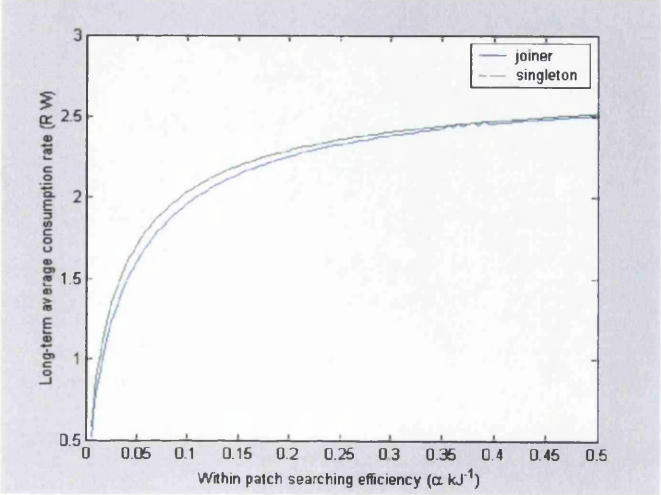

CHAPTER 8

GENERAL DISCUSSION

Theoretical models have been used extensively for the study of foraging theory. Although they can never replace empirical work for the study of any natural system, they offer a valuable tool for gaining insight into the underlying principles of animal behaviour. They are useful because they allow researchers to remove the unpredictable variables encountered in the environment. Unlike many other disciplines in the natural and physical sciences, animal behaviour is heavily influenced by the state of the environment. Small inconsistencies between experimental sets can lead to a huge disparity in the results. Researchers can never control for all eventualities. Laboratory experiments attempt to minimise this, by removing external factors and maintaining equality between sets. But conversely, this may confound results even further because the environment is now so hugely different from the natural one that animals may not behave naturally at all. By their very nature theoretical models are entirely conceptual, and this is an issue that causes much debate because of their divergence from reality. But it is for this very reason that they are so useful. Theoretical models provide a vastly simplified representation of the environment, in which all unpredictable aspects are controlled for and the only varying factors are those which are varied by the experimenters, without any risk of upsetting the animals involved, because there aren't any.

In this thesis I use several theoretical models to examine an aspect of foraging theory that has roused much interest in recent years. At its simplest, public information theory suggests that animals in groups are likely to reap benefits if they share information about the available food resources. However, the existing theory makes several assumptions and simplifications that are not likely to hold true in nature. First of all, the original public information model (Valone, 1993) contains inconsistencies concerning the depletion of food patches that makes the published results questionable. Secondly, much of the theory assumes that information is delivered completely and without error or cost. Thirdly, the method by which models simulate patch estimation in foraging groups makes unrealistic assumptions as the size of a group increases. In very large groups these assumptions are likely to depart wildly from nature and cannot be used to accurately predict animal behaviour. Finally many foraging models also ignore spatial considerations, particularly in terms of travelling in-between food patches. The aim of my thesis is to re-examine the theory behind public information use in groups of foraging animals, and to explore the

consequences of sharing public information when these simplifications are removed and re-addressed.

I firstly examine, in Chapter 2, the scientific literature covering social foraging and information sharing. I discuss the benefits that foragers may experience from others, as a result of sharing information. This covers four main themes: patch discovery rates and travelling time (local enhancement or area copying), the acquisition of novel food-obtaining behaviours (behaviour copying), stealing or scrounging (kleptoparasitism), and patch estimation. I examine some of the empirical evidence supporting each of these, and also the limitations of each of these studies. I pay particular attention to the use of social information for patch estimation, termed public information, which forms the foundation of this thesis. I consider the means by which public information signals might be realistically transmitted in the natural world, and how it may be used throughout the animal kingdom for not only the assessment of food patches, but also for the selection of breeding habitat, and potential mates and competitors. I also examine the evidence demonstrating the sensory and cognitive limitations that animals face, how this may affect their ability to gather public information reliably and accurately.

The first model to fully examine the effect of public information in foraging groups was published by Tom Valone in 1993. He envisioned a scenario in which a group of foragers travel in a tightly cohesive group, between a number of isolated and depleting food patches. On entering a patch individuals begin feeding, signalling to each other member of the group every time they made a successful prey discovery. With this information, each individual is able to create an estimation of the decreasing patch quality based upon how long the group has spent in the patch, and how many prey items have been found collectively by the whole group in that time. Valone bases his model upon a formula developed by Iwasa et al (1981), which does the same thing for a lone forager. He compares this to groups that do not share information, and thus contain individuals that have estimates based upon their own foraging success alone, and therefore may be very different from forager to forager. To maintain group cohesion he employs three strategies that decide when the group should quit each patch. He compares the long-term foraging success and patch

quitting ability of forages sharing public information, against those using one of the three patch quitting strategies.

Iwasa et al's estimator function relies on the assumption that the rate of finding food within a patch is inversely proportional to the number of prey remaining, i.e. as food becomes scarce, it is harder to find. For some reason Valone (1993) incorporates a different prey depletion rate, which makes the estimator unreliable and his results questionable. In Chapter 3 I re-evaluate this work, constructing a model that remains consistent with Iwasa et al's (1981) formula. I assess the value, in terms of long-term foraging success, of public information use for group foragers. For comparison, I adopt two of the patch quitting strategies used by Valone (1993), and introduce a third, proposed by Ruxton (1995a), for groups not sharing public information. I demonstrate that groups sharing public information are not more successful in the long-term than lone foragers. The rate of patch depletion increases with group size, but this is balanced by the rate at which such groups discover food patches, which decreases with group size. The result is that groups experience the same feeding rate and patch quitting ability as lone foragers, regardless of group size.

However, groups sharing public information *are* more successful than groups that do not share public information. Groups comprising individuals that rely solely on their own sampling information to estimate patch quality often experience conflict over when to quit a patch. Each individual has its own estimate depending upon its personal foraging success within a patch, and will likely want to leave at a different time. The patch quitting strategies employed by the group solve this problem, by selecting one or two individuals (depending upon the strategy) to determine when the group quits. The decision to quit is therefore entirely dependent upon the success of a particular individual – in two of the strategies these happen to select individuals from the lowest end of the distribution of patch estimates; i.e. those which want to quit the patch first. Thus the group is vulnerable to quitting as a result bad luck, rather than genuine poor patch quality. The third strategy minimises this because it relies on the estimate of one individual, which remains consistent across all patches visited. This individual will experience both good and bad luck, and so on average will possess the correct patch estimate and the group will quit on average at the correct time. But since this is only the average, and the group is still susceptible to bad luck on

occasion, the actual quitting time from each patch will be quite variable. Sharing public information removes this indecision from patch quitting, since all individuals have the same knowledge and groups are no longer vulnerable to bad luck.

A consequence of using foraging time inefficiently is that animals experience a lower rate of gain from the environment they are feeding in. In the same way that increasing the average travel time between patches increases the time a forager should spend in a patch before quitting (Charnov, 1976) in order to make up the cost of travelling, wasting time in poor patches and not utilising profitable patches to their full potential means that foragers should also seek to exploit each patch more fully. Thus, the groups not sharing public information but relying on some quitting strategy to initiate patch departure are immediately disadvantaged, since they are forced to remain longer in each patch they visit. Combined with this, the fact that they cannot accurately estimate patch quality means that they *cannot* quit patches at the optimal quitting value and they often quit patches far too early. Finding the correct patch quitting value is clearly crucially important.

This highlights the importance of familiarity with the environment (Griffiths et al, 2004), and the knowledge of the average rate of gain expected from it (i.e. the marginal value). Some previous models of public information theory (Valone 1993; Ruxton 1995b) assume an arbitrary patch quitting value that bears no relation to the marginal value of the simulated environment. Foragers cannot hope to forage optimally under these conditions. If an animal knows its environment it will presumably have knowledge of the distribution of prey resources in it, and will know the average rate of gain that it can expect to achieve from the environment as a whole (i.e. the marginal value). They can therefore attempt to quit patches at this value, in the hope of foraging optimally. However, if they are not familiar with their environment, or misinformed about its richness of prey, they will be aiming to quit patches at a sub-optimal patch value. If they are not sharing information and therefore already constrained in their ability to quit patches accurately, they will clearly suffer further because they will never be able to make up this initial cost.

The model presented in Chapter 3 is based upon a formula developed by Iwasa et al (1981), which estimates the remaining number of prey items in a food patch, given a

knowledge of the prey distribution throughout the environment, the time spent in the patch, and the number of prey already found there. This model was originally designed to simulate the foraging activity of a lone forager. In Chapter 3 I present a modified version of this model to accommodate foraging groups. Like Valone (1993) I assume that foragers sharing public information are made aware of all prey capture events, and so have complete up-to-date information of the collective group foraging success. Foragers not sharing public information do not have this luxury, and must estimate group foraging success using other means. A simple method, again following Valone (1993), is to let each forager assume that all others in the group experience the same foraging success as itself. For example, if it finds a prey item it assumes that every other forager has also found a prey item. In small groups this may not be particularly unrealistic, but as group size increases it becomes more and more unlikely. Additionally, as group size increases, when each prey item is found it becomes less and less likely that any given individual has found it. Using this method of patch estimation therefore becomes very unreliable in large groups. In Chapter 4 I present a model that removes the bias imposed on individual patch estimation in large groups.

In Chapter 4 I examine the foraging success and patch quitting ability of animal groups not sharing public information, and using the same three patch quitting strategies examined in the previous chapter. I show that using the new model, foragers are much better able to estimate patch quality. Overall they are able to quit patches at the given marginal value, regardless of group size. This is a marked improvement on the previous model, where foragers were quitting patches progressively earlier with increasing group size. In smaller groups, there is no clear difference to prey capture rates, as we would expect, since the bias imposed by the previous model was only expected in large groups. Where group size is large the new model shows that in some situations foragers experience higher prey capture rates than previously, whereas in others they experience lower capture rates. Despite their improved ability to estimate patch quality, foragers in large groups experienced a much more variable ability to quit patches. Although they were able to quit patches according to the marginal value theorem overall, this was in fact highly variable from patch to patch. The variability of patch quitting increases with group size.

By removing the bias imposed on patch estimate in large groups, the new model ensures that each member of a foraging group is likely to have a much more similar estimate of patch quality than with the previous model. Rather than making rash assumptions based upon personal foraging success and the number of individuals in the group, it takes into account the number of search attempts made and the relative likelihood of success on each. Thus all foragers hold a similar, and more realistic estimate of patch quality. This offers an advantage in larger groups, because they are better able to quit patches at the marginal value. However, this similarity in patch estimation means that if a mistake is made, it is unlikely to be corrected and the group could end up quitting patches at any time. Patch quitting thus becomes highly variable.

Since animals have only a limited brain size, their cognitive attention will be similarly limited. The neuronal resources available to them will need to be divided between all physiological processes, body functions and behaviours. The ability of animals to share and utilise public information will therefore also be dictated by their cognitive processing powers and the limits to their sensory attention. Many experimental studies have shown that as animals divide their attention between two or more tasks, their competence at each one diminishes (Vreven and Blough, 1998; Lima and Bednekoff, 1999; Dukas and Kamil, 2000; 2001). There is therefore likely to be a cost to information acquisition, as animals divide their attention between gathering public information and personal foraging. Most previous models of information sharing ignore this restriction, as do the models described in Chapters 3 and 4 of this thesis. In Chapter 5 I present a model that examines the consequences of public information use when sensory attention is limited and must be divided between two behaviours. Building on my existing public information model, I assume that animals foraging in groups have access to information of all prey capture events occurring within a patch. However I build upon the previous models and impose a cost for this information use. Animals divide their limited attention between two tasks, and the cost to information acquisition comes in terms of reduced personal foraging success. As a forager directs more of its attention towards scanning for public information signals, it becomes less likely to notice a prey item when it encounters one.

Using the results obtained during simulations with the models in Chapters 3 and 4, I predicted the cost values that I would need to impose on groups sharing public information, before their foraging success decreased to those of the groups using each of the patch quitting strategies. I demonstrate that the actual cost values required to do this are higher than predicted. In other words, there is a point at which foragers are gaining public information and not paying for it. As a forager pays a cost to information gathering, it stands a chance of not detecting a prey item that it has uncovered. The prey item therefore remains un-caught, and the group must spend a longer period of time in the patch before quitting. As foragers divert more attention towards scouting for public information, so they spend more time in the patch. As it stands we can predict the cost easily, as the two should be directly proportional. However, the cost does not affect the time spent travelling between patches. Travel time remains unchanged, and so the total time spent foraging by groups that are paying a cost to information acquisition increases less than proportionally.

As a result of this there is a point at which foragers sharing public information are receiving a payoff above the non information patch quitting strategy, but which they are not paying a cost for. I call this residue, the willingness for public information use. The larger this residue, the more willing foragers should be to using public information, and the more benefit they should receive for no extra cost. I present a formula that allows us to calculate this cost, for any given set of parameter values.

A second limitation likely to be imposed upon an animal's use of social is that of information fidelity. An animal will make decisions and perform behaviours dependent upon its own internal state, and perception of the environment. Animals paying attention to behavioural signals provided by another will receive information that is biased towards that individual, and therefore misleading or inaccurate. The information an animal receives will also be subject to elements of the physical environment and configuration of the group that it's in, both of which may cause interference and disruption to the transmission of such information. Obstacles in the environment may cause signals to be lost; this is especially likely in rough terrain, or heavy foliage, or where there are many individuals within a foraging group. Alternatively, an animal may perceive a signal from some neutral source, which it misinterprets as a public information signal. Since an animal's performance is

reduced when it divides its attention between two or more tasks (Vreven and Blough, 1998; Lima and Bednekoff, 1999; Dukas and Kamil, 2000; 2001), it seems likely that an individual will make mistakes in identifying public information signals if it is dividing its attention between personal foraging and scouting for information.

In Chapter 6 I examine the benefits of public information use when information is erroneous or incomplete. I describe a further modified version of the public information model, in which all foragers in a group have access to information indicating the successful prey capture events of each individual. However each time a prey capture signal is transmitted, there is a chance that the members of the group do not receive it. In this case, only the forager finding the food item will be aware of it. There is also a chance that a forager will transmit a false signal – indicating a prey capture event that did not occur. This signal is received by all members the group. Thus, each member of the group makes its estimate of patch quality based partially upon false or incomplete information. I demonstrate that whilst the long-term foraging success of animals is severely hampered when animals are faced with public information containing false signals, missing true signals barely has any effect except when misses occur at almost every opportunity. I envision a prey environment with food patches that contain either very few or very many prey. When a forager finds a food item it is therefore quite likely that it has found a rich patch – the more prey it finds, the richer the patch is assumed to be. By transmitting false signals foragers are deceived into thinking even poor or empty patches are rich, and they remain foraging there without making any gain. In rich patches, they are misled into thinking the patch is richer than it truly is, but also that they are depleting it more quickly than they really are. They have knowledge of how many prey the patch should contain, and with false prey capture signals they estimate that they exhaust the patch sooner than have done so. Quitting rich patches too early and remaining in poor patches for too long must have serious consequences for foragers attempting to maximise their long-term prey intake rates.

On the other hand, foragers missing signals will tend to underestimate the true quality of a food patch, because they are not aware of all the prey capture events that have been made. The group foraging success will be higher than they realise. Under-estimating a patch will however induce them to quit a patch early. But where signals

are only missed from time to time, and foragers are able to find food relatively easily, this will not affect patch departure too greatly because they will not be too misguided about the true quality of the patch. Missing signals is only detrimental when it happens on almost every prey capture, because regardless of how many prey items are discovered in the patch the group remain unaware of it, and therefore assume the patch is very poor or empty.

The chapters in this thesis have so far concentrated upon the activity of foragers within food patches: specifically the estimation of patch quality and patch quitting ability, under different circumstances. I have assumed that the movement and activity of foragers between patches is identical – i.e. that the time it takes to locate and travel to a new food patch is inversely proportional to the size of the group. This is a useful simplification for the models introduced in the previous chapters. Unfortunately, it is unlikely to occur so conveniently in nature. Non-spatial models such as these neglect important aspects of the environment (Ruxton, 1995a; Ruxton and Glaseby, 1995). For example, a group of animals are at a higher density just after they quit a patch, than they are once they have dispersed into the environment. When a number of foragers are searching a small area, it is very likely that some parts of the environment will be examined more than once (Ruxton, 1995a; Ruxton and Glaseby, 1995). This is called search overlap, and immediately suggests that the rate of discovering new patches will not be inversely proportional to the size of the group. A further quandary is that of dispersal. As foragers spread out into the environment searching for patches, the average distance between them increases. When a new patch is discovered it will take longer for some individuals to reach it, than it will for others. This creates a further problem, in that by the time the individuals travelling further have finally arrived at the patch it will already have been partially depleted of its prey resources. There will therefore be some critical distance beyond which it is not beneficial for a forager to travel towards a newly discovered patch, when it can continue searching for its own patch.

In Chapter 7 I examine a game-theoretical model which can be used to analyse the joining policies for an individual searching for food patches, under different group foraging scenarios. First of all I examine the optimal behaviour for single forager, in an environment where food patches are scarce. I imagine that a food patch has been

discovered and a forager has entered it. Since a patch is finite in value and prey is not replaced once eaten, the intake rate of the forager decreases over time. If an animal is to maximise its long-term feeding rate, there is an optimal time at which it should quit the patch. Using this model I demonstrate that there is only one solution for any given ecological situation – i.e. only one marginal value. As the rate of finding food or the average time spent between patches increases, so the time before quitting increases – the forager should spend longer in the patch. This agrees well with classical optimal foraging theory (Charnov, 1976; Iwasa et al 1981; Green, 1980, 1988).

The second scenario envisages two foragers: one of which has discovered a food patch. The other now has the choice to either travel to it, or continue searching for its own patch. While the first forager remains feeding in the discovered patch, its value decreases as prey is harvested from it. The longer it takes for the second forager to reach the patch, the lower it's value will be, and the lower the return to the second forager. The second forager should only travel to and join the patch, if its feeding rate will be above the long-term expected feeding rate by doing so. The model shows that as the average time spent travelling between patches increases, the critical joining distance also increases. As patches are farther apart, it is more attractive to join a newly discovered patch even though they have been partially depleted. Conversely, when the average travel time is smaller and patches are closer together, a forager should be more willing to find its own patch than to join a discovered one. Overall prey availability in the environment does not affect the joining distance: although it does affect the foraging success of each individual.

In the third scenario I carry this model further, and imagine a scenario in which there may be many foragers. When any forager joins a discovered patch, several others may have arrived there already, depending upon the density of foragers in the environment. As each individual arrives, the rate of patch depletion increases until at some point all individuals within the critical joining distance will have entered the patch. Each consecutive forager will reap lower returns than the one before. A forager at the critical joining distance will reap the lowest returns of all. As forager density increases, so the critical joining distance decreases. Overall, foraging efficiency will decrease because more time will be spent travelling between patches,

relative to gain. As the initial value of a patch increases lone foragers fare better than those in groups. Prey capture rates increase for both lone foragers and those in groups, but dividing the available resources between several foragers means that each acquires a smaller share. If foragers are able to travel faster to patches once they have been discovered the critical joining distance increases, as they will be able to reach far away patches more quickly and will not harvest each patch so intensely before quitting. On the other hand, the average time spent in-between patches increases, discovered patches will be attractive from further away but they will be harvested to a lower level, to make up the extra travelling cost. Increasing the searching rate within a patch will have a similar effect to increasing forager density. Patches will be exhausted more quickly before a forager arrives there, and since it will be able to harvest food from a patch it discovers itself, it will be less willing to join one discovered by others.

Several questions arise from the work carried out in this thesis. I have tried to relax some of the constraints introduced in previous models of public information use, but I continue to make several assumptions for convenience and simplicity. Perhaps the most important of these is the assumption that the time spent travelling between patches will be inversely proportional to the size of the group. In Chapter 8 I investigate the searching and joining behaviour of foragers between patches, and although I do not examine the relationship between group size and travel time *per se* my findings indicate that this will be affected by spatial distribution of food resources but also by spatial distribution of foragers when a patch is discovered. It seems likely that the specific ecology of an animal group as well as factors in the environment will be crucial elements influencing travel time. Theoretical models such as Ruxton (1995a) make an attempt to discover general predictions of the travel time relationship, but empirical studies are scarce and severely limited. This is one area that needs to be studied further experimentally, in order to look for both general rules but also to examine the effects of specific ecology.

A further finding from Chapter 8 emphasises that individuals are unlikely to enter a patch simultaneously - yet another simplification made throughout this thesis is that groups will maintain strict cohesiveness. This was done purely for the convenience of calculating prey capture rates and ensuring equality between foragers. Chapter 8

suggests that the further forager disperse into the environment the less likely they are to enter a patch simultaneously, and indeed the more likely the group will fragment. Both of these assumptions would ideally be addressed together, but it seems intuitive that a model considering these will not add any evidence in favour of public information as a factor promoting aggregation.

Another point raised here is what exactly constitutes a patch. This is a tricky question to answer, but is crucial to the understanding of patch estimation. In Chapter 2 I meention a number of studies in which the researchers definition of a food patch may not be shared by the animals under investigation. This will clearly have serious implications as to how the behaviour of animals are interpreted. Take for example Smith et al (1999), who investigate information sharing in crossbills. The experimental set up dictates that the birds are housed in an aviary with a mesh divider separating the subject and partner birds. Artificial trees in the centre of the cage were fitted with a number of pinecones, in such a way that the mesh split the tree in half - half on one side of the mesh (containing the subject bird) and half on the other side (containing the partners). From the birds point of view, what precisely is a patch? The authors intended that each tree was a patch, but was this mirrored by the crossbills? Did the birds perceive each pinecone as a patch? Did the mesh interfere with their perception of the trees being the same food resource, of different ones? Questions like this need to be answered if we are to gain complete understanding of an animals behaviour. Again, understanding the ecology of an animal will be crucial to answer them. Theoretical analysis can only take this work so far - empirical investigagion is required to answer such specific questions.

How one would go about measuring exactly cognitive and attentional limitations is yet another question raised by this thesis. In the work here the mechanisms by which animals detect and process sensory information is ignored, but this is precisely the type of thing that researchers need to consider if further insight is to be gained. Studies such as those of Dukas and Kamil (2000, 2001) are priceless examples of how this can be achieved. Experimental psychology has a lot to offer this area of behavioral ecology.

On the other hand, the field of robotics could prove an invaluable (and as yet largely ignored) instrument in behavioural ecology. Robots would make ideal subjects to examine information acquisition in a cluttered environment. They have an advantage in that the limits to their sensors and sensor fields do not have to be designed, and interference through noise and obstructions in the environment are similarly intrinsic. Whatsmore, a vast range of data can be easily stored and recorded for analysis - something that is very difficult to achieve with animals.

During the course of this thesis I have developed a series of models that can be used to examine various aspects of social foraging and public information use. In two chapters I reconsider early published models and offer new insights that may make them more relevant to natural ecological situations. In two further chapters I discuss new models in an attempt to investigate the problems experienced by social foragers when faced with sensory and cognitive limitations. Finally, I take a step back from the activity of foragers within patches and examine their movement through the environment. I have discussed the validity of all these models, the value of their predictions for natural conditions and also their limitations.

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